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## NUMERIC ANALYSIS OF THE LIZARD GENUS *SCELOPORUS* WITH SPECIAL REFERENCE TO CRANIAL OSTEOLOGY

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**ABSTRACT.**— Numerical statistical methods were used to analyze the species in the genus *Sceloporus* using cranial osteology, external meristic and numeric characters, karyology, display behavior, and geographic distribution.

A new classification for the genus is proposed with three major branches or groups. Group I contains 7 species in 3 species groups. Group II contains approximately 19 species in 5 species groups. Group III contains approximately 32 species in 5 species groups. This classification is supported by the cluster analysis of several different sets of data. Cranial osteology, zoogeography, behavior, and karyology are shown to be taxonomically significant as numeric characters. Stepwise discriminate analysis shows that this classification of the species of *Sceloporus* into 3 major groups and 13 species groups is significant at the .999 confidence level: It is concluded that the 3 major groups should be given taxonomic recognition.

Cope (1900) stated, "The distinction of many of the species of this genus [*Sceloporus*] is not accomplished without difficulty. I recommend it as an excellent *pièce de résistance* for those persons who do not believe in the doctrine of derivation of species." This statement was endorsed by Hobart Smith (1938:548-49):

*Sceloporus* is one of the most nearly ideal of living genera of reptiles for the study of speciation and related phenomena. The characteristics which it possesses and which are essential to an ideal genus for such studies are:

1. *A large number of living forms.* . . .
2. *Prolificity.* Where *Sceloporus* occurs, usually it is the most common of all reptiles, or for that matter, of all vertebrates.
3. *A large range, entirely contiguous.* The genus occupies practically all of the United States, and occurs as far south as Panama.
4. *Great adaptability.* Species in this genus have adapted themselves to considerable range of elevation—from below sea level (Death Valley) to about 13,500 feet above sea level. They occur in almost every conceivable terrestrial habitat—deserts, sand dunes, forests, on rocks, trees, or ground in grassy plains or heavy brush, and even on houses, fences and other man-made structures.
5. *Lack of obvious distinctive specific characters.* Subspecies are numerous and species not so well defined as in many other genera of animals, and for this reason relationships may more definitely be postulated.

These characters are indicative of a group of relatively recent development.

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Smith would probably have added a sixth and seventh characteristic if karyological and behavioral information had been available.

It is only proper, in consideration of the foregoing, that *Sceloporus* should be considered a suitable candidate for the application of recently developed statistical methods.

The study here reported was undertaken with several questions in mind: (1) What is the most natural arrangement of species within the genus? (2) Can satisfactory results be obtained with modern statistical methods? (3) Can significant intrageneric taxonomic information be obtained from the cranial osteology of *Sceloporus*? (4) Will different sets of characters (scale counts, external morphology, karyotypes, behavior, osteology, etc.) produce similar results? (5) Is *Sceloporus* a single genus?

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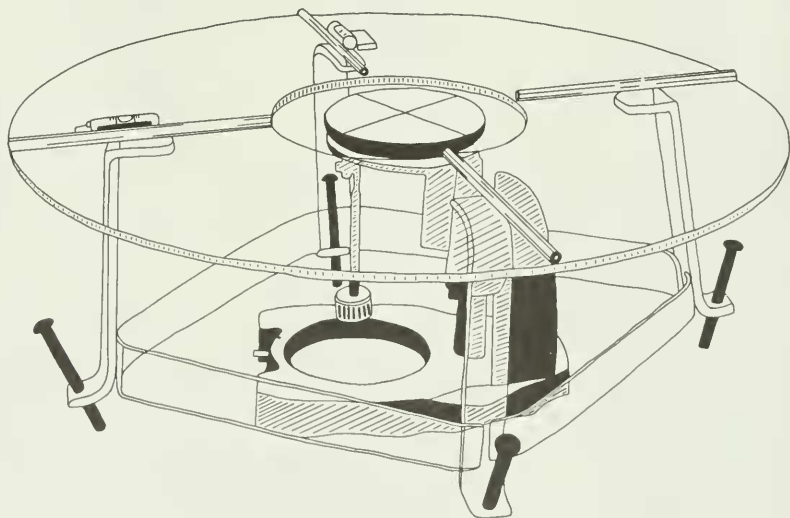


Fig. 1. Platform for constant angle photography of skulls.

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## REVIEW OF LITERATURE

### Taxonomy

The term *Sceloporus* was coined by Weigmann (1828:369-70) from the Greek words *scelos* (leg) and *porus* (hole). Our translation of Weigmann's original description follows:

Furthermore, there is a Mexican genus with many species which is similar to *Tropidurus* in body shape, head shape, placement of nostrils and ears, formation of teeth, and form and placement of dorsal and caudal scales.

But it differs in that it has femoral pores and the dorsals are enlarged. Both genera have a peculiar dermal pocket on the side of the neck. This dermal pocket is crescent shaped in the new genus. It is formed by a fold in the skin

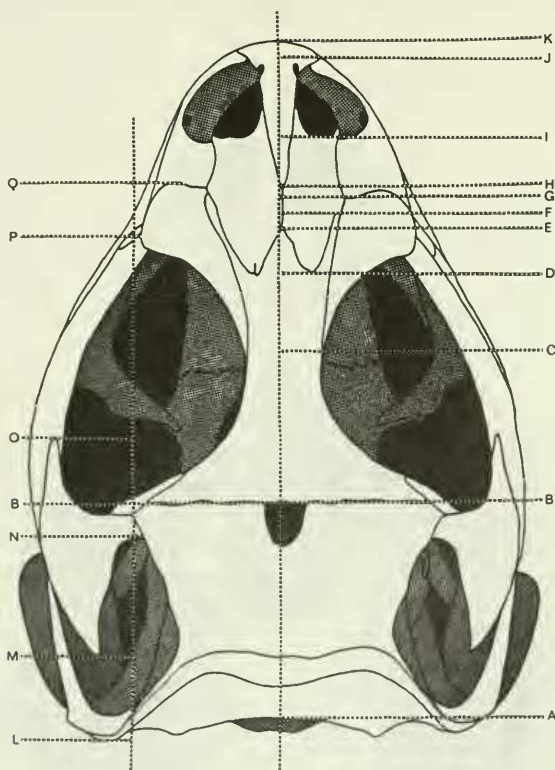


Fig. 2. Characters 41 to 50 on dorsal view of skull.

41 = $\frac{A-B}{B-E}$	42 = $\frac{E-H}{B-E}$	43 = $\frac{H-K}{B-E}$	44 = $\frac{D-F}{F-G}$	45 = $\frac{G-I}{B-E}$	46 = $\frac{I-J}{B-E}$	47 = $\frac{B-P}{B-E}$
48 = $\frac{L-N}{A-B}$	49 = $\frac{M-O}{N-B}$	50 = $\frac{C-G}{P-Q}$				

and the inner surface is lined with shagreen-like scales. I usually found a population of 6-legged orange-colored epizoa in the dermal pocket in which case the scales would be missing.

His Highness, the Prince of Neuwied observed the same thing in his description of *Tropidurus torquatus* (Beitrag zur Naturgeschichte Brasiliens I. p. 148).

Hernandez has already mentioned 2 of the species of this genus. He reports that the species which can reasonably be considered typical is a crevice-dweller and eats worms. Because of the large femoral pores, I name this genus *Sceloporus*. The following is a short provisional description of the species.

Weigmann (1828) then gave a short description of the genus and six species: *torquatus*, *spinosus*, *grammicus*, *pleurostictus*, *aeneus*, and *scalaris*. In the heading, he provided the common name *Stone Lizard*, which name he explained in a footnote: "I have chosen this German name (Stone Lizard) because Hernandez says that the common species of this genus are called Tecoixin in Mexico. Tecoixin means Saxorum Lacerta [*Saxorum lacerta* = stone lizard]."

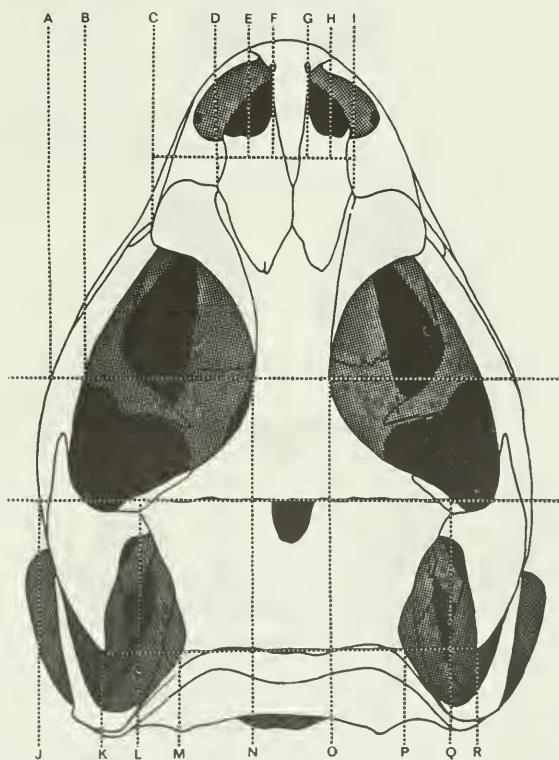


Fig. 3. Characters 51 to 56 on dorsal view of skull.

51 =  $\frac{N-O}{L-Q}$     52 =  $\frac{J-L}{L-Q}$     53 =  $\frac{M-P}{L-Q}$     54 =  $\frac{K-M}{L-Q}$     55 =  $\frac{D-C}{D-I}$     56 =  $\frac{F-G}{E-H}$



Hobart Smith (1938:547-48) provided an excellent history of the revisions of this genus which is paraphrased as follows:

Weigmann (1834) recognized nine species—*torquatus*, *formosus*, *spinosus*, *horridus*, *grammicus*, *microlepidotus*, *variabilis*, *aeneus* and *scalaris*. Dumeril and Bibron (1837) recognized 10 species, adding *undulatus* Latreille. Bocourt (1834) recognized 22 species. Cope (1885) published a synopsis of *Sceloporus*, in which he recognized 36 species and subspecies.

Boulenger (1885) recognized 33 species and subspecies and Gunther (1890) recognized 30 species and listed 7 other described forms without comment as to validity.

Boulenger (1897) presented his conclusions with regard to the species of *Sceloporus* in his revision of the genus and recognized 36 species and subspecies. . . .

In the last monograph of the genus is that of Cope (1900) published in 1900, in "The Crocodilians, Lizards, and Snakes of North America." Forty species and subspecies are recognized.

Smith (1939:29) added, "Of the 127 names proposed in the genus, I consider 95 valid. These have been segregated into 15 groups of approximately equivalent morphological value."

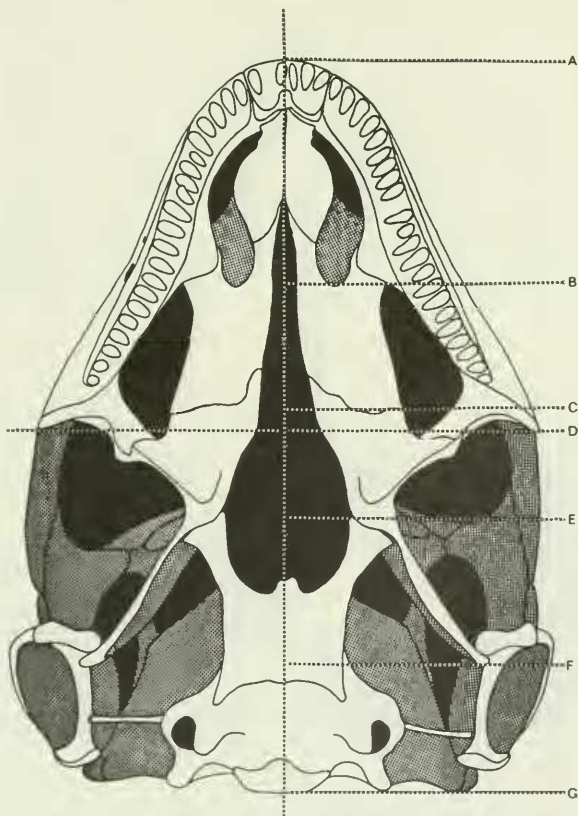


Fig. 4. Characters 57 to 60 on ventral view of skull.

57 =  $\frac{G-E}{A-D}$     59 =  $\frac{C-B}{A-D}$     58 =  $\frac{E-D}{A-D}$     59 =  $\frac{C-B}{A-D}$     60 =  $\frac{F-D}{A-D}$

Smith and Taylor (1950) provide the following list of groups and species (15 groups, 54 species; in each, the first species is the group name): (1) *formosus*, *malachiticus*, *asper*, *stejnegeri*, *presygous*, *lunaei*; (2) *spinosus*, *lundelli*, *edwardtaylori*, *melanorhinus*, *clarki*, *orcutti*, *magister*, *horridus*, *olivaceus*; (3) *undulatus*, *cautus*, *occidentalis*, *woodi*; (4) *graciosus*; (5) *grammicus*, *heterolepsis*; (6) *megalepidurus*, *pictus*; (7) *torquatus*, *serrifer*, *mucronatus*, *poinsetti*, *cyanogenys*, *bulleri*, *lineolateralis*, *ornatus*, *dugesii*, *jarrovi*; (8) *variabilis*, *cozumelae*, *teapensis*, *parvus*, *couchi*; (9) *merriami*; (10) *maculosus*; (11) *chrysostictus*; (12) *siniferus*, *squamosus*, *carinatus*, *ochoterenai*; (13) *utiformis*; (14) *scalaris*, *jalapae*, *aeneus*, *goldmani*; (15) *pyrocephalus*, *gadoviae*, *nelsoni*.

Later, Smith and Taylor (1966) added four new species to their checklist: *macdougalli*, *shannonorum*, *subpictus*, and *virgatus*. Hall (1971) increased the number of species in this genus to 61 by recog-

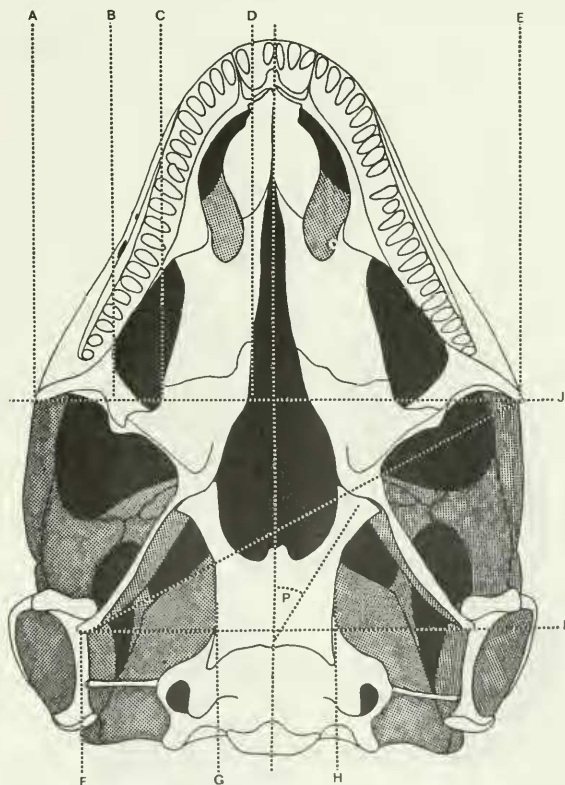


Fig. 5. Characters 61 to 66 on ventral view of skull.

$$\begin{array}{ccccccc}
 61 = \frac{A-B}{A-E} & 62 = \frac{B-C}{A-E} & 63 = \frac{C-D}{A-E} & 64 = \frac{G-H}{A-E} & 65 = \frac{E-F}{I-J} & 66 = \frac{(\text{diagonal})}{5(\text{Tangent P})}
 \end{array}$$

nizing *acanthinus* and by adding *exsul* and *insignis*. Hall (pers. comm.) has called attention to a new species in Baja California and has suggested the elevation of *magister zosteromus* and *orcutti licki* to specific rank. He has also proposed that *grammicus* contains at least six cryptic species. Hobart Smith (pers. comm.) also has a manuscript species. A second manuscript species described by Smith and Larsen is in press. If these new species are included, the total number in this genus would exceed seventy.

**Osteology.** Avery and Tanner (1971) presented a review of lizard osteology to which the reader is referred. On page 6 they stated:

In summary the literature dealing with anterior osteology and myology of lizards is scattered and varied. Descriptions of skulls representing almost all families can be found. With the exception of such papers as Camp (1923), McDowell and Bogert (1954), Savage (1958), Etheridge (1964), and Presch (1969), little has been done, utilizing osteology, to analyze the evolutionary lines within families.

Of the above listed papers, only Savage, Etheridge, and Presch considered Sceloporine relationships, and none of these reported on species relationships within the genus *Sceloporus*.

Cope (1900:330-31) described the cranial osteology of *Sceloporus* on the basis of two specimens of *undulatus* and one specimen of *spinosus*. He described the following 35 characteristics:

[1] Premaxillary bone has a long superior spine and is [2] truncate on the palatal face, and [3] has the button-like process. [4] The nostrils are partially vertical, so that the [5] nasals are a little shortened in front. [6] The latter are rather large and are distinct. [7] The frontal is simple and narrow and is [8] strongly grooved on the middle line below. [9] The parietal is short and wide, and [10] is perforated by a large pineal foramen, [11] which touches the

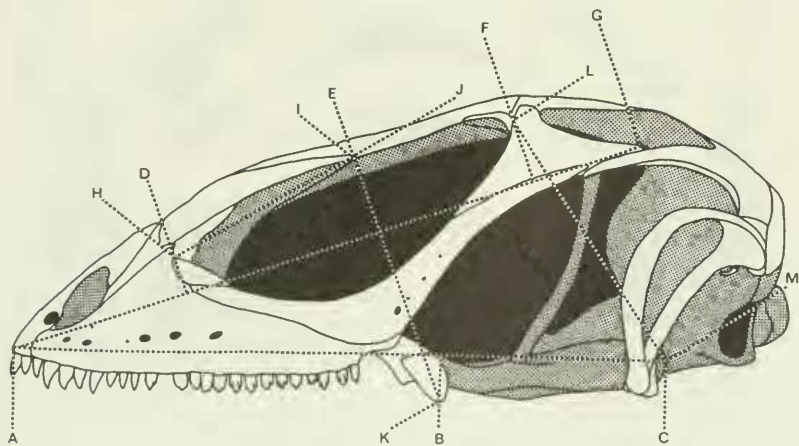


Fig. 6. Characters 67 to 73 on lateral view of skull.

$$\begin{array}{ccccccc}
 67 = \frac{A-B}{A-G} & 68 = \frac{B-C}{A-G} & 69 = \frac{A-D}{A-G} & 70 = \frac{D-E}{A-G} & 71 = \frac{E-F}{A-G} & 72 = \frac{H-I}{D-E} & 73 = \frac{J-K}{L-M}
 \end{array}$$

coronal suture. [12] Parietoquadrate arch distinct. [13] Supraoccipital broadly but loosely attached [14] confluent with exoccipitals. [15] Prefrontals large, not reaching postfrontals above. [16] Lachrymal small and joining jugal. [17] Postfrontal a small splint. [18] Postorbital large, extensively in contact with jugal and supratemporal. [19] Paroccipital small. [20] Vomers short, divaricate, and separated by a deep notch behind. [21] Palatine with the vomerine process longer than maxillary; [22] Palatine foramen large. [23] Palatines and pterygoids well separated from each other on the middle line; [24] ectopterygoid deflected at its internal extremity. [25] Basispterygoids developed. [26] Quadrate with two conchs [27] the internal the narrower. [28] Presphenoid rudimental; [29] sphenoid and basioccipital coossified; [30] descending lateral processes of the latter strongly developed. [31] The supraforaminal part of the petrosal is very short; [32] the infraforaminal portion is produced beyond it and is nearly horizontal in position. [33] The foramen of the eighth nerve is at the bottom of a fossa. [34] Epipterygoid resting on pterygoid much posterior to ectopterygoid and reaching parietal without touching petrosal. [35] Occipital condyle not subdivided by grooves.

(We disagree with the last characteristic as most of our specimens exhibit a conspicuous pair of grooves that subdivide the occipital condyle.)

Lundelius (1957) produced the only computerized statistical analysis of *Sceloporus* cranial osteology to date. On pages 67 and 68, he listed 32 cranial measurements used in his analysis:

(1) midline length of premaxillary, (2) midline length of nasal, (3) midline length of frontal, (4) midline length of pineal, (5) midline length of parietal, (6) total length of skull roof from snout to posterior edge of parietal, (7) inter-narial width, (8) width anterior to orbit, (9) interorbital width, (10) anterior width of parietal, (11) width of pineal, (12) interfenestral width, (13) maximum width of temporal fenestra (diagonal), (14) distance from basicranial tubera to

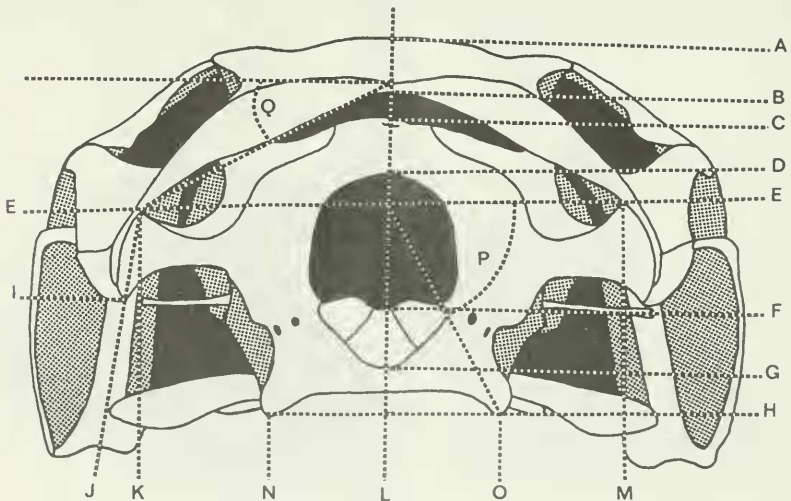


Fig. 7. Characters 74 to 80 on posterior view of skull.

$$\begin{array}{l}
 74 = \frac{C-D}{A-B} \quad 75 = \frac{D-F}{A-B} \quad 76 = \frac{F-G}{A-B} \quad 77 = \frac{E-I}{A-B} \quad (\text{along diagonal J}) \quad 78 = \frac{K-M}{N-O} \\
 79 = 5(\text{Tangent P}) \quad 80 = 5(\text{Tangent Q})
 \end{array}$$

basipterygoid process, (15) length of palatine ramus of pterygoid, (16) length of palatine, (17) length of prevomer, (18) length of quadrate ramus of pterygoid, (19) width across basicranial tubera, (20) width across basipterygoid processes, (21) width across posterior ends of maxillaries, (22) width across descending processes of pterygoid, (23) width across anterior part of palate, (24) tooth row width of premaxillaries, (25) length of maxillary, (26) distance from the posterior end of maxillary to posterior edge of quadrate, (27) length of quadrate, (28) total width of skull across exoccipitals, (29) length of exoccipital, (30) medial end of exoccipital to lateral edge of foramen magnum, (31) width of foramen magnum, (32) width of occipital condyle.

Our analysis utilized all the above measurements, or functions of them, with the exception of numbers 4, 11, 13, 14, and 23. Numbers 4 and 11 were omitted because the thin bone around the parietal foramen is easily dissolved in bleach and because we suspect that the dimensions of the parietal foramen may be affected by the time spent in bleach during preparation. Number 13 was omitted because it is a diagonal with no definite points of origin. We measured the width of the temporal fenestra at right angles to the midline. Numbers 14 and 23 were omitted because they are difficult to define on a photograph (see material and methods below).

### Karyology

The karyology of *Sceloporus* has attracted much interest because of the high level of intrageneric variation. Gorman, Atkins, and Holzinger (1967) published karyotypic data on 15 genera. On page 287 they reviewed a manuscript presented by William P. Hall:

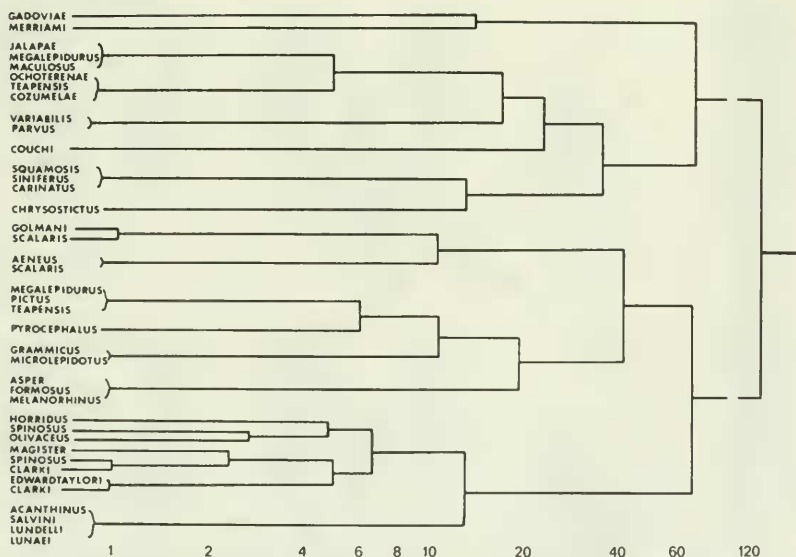


Fig. 8. Dendrogram produced by Ward's cluster analysis of Smith's (1939) data for *Sceloporus*.



Hall (1965) has summarized all available information on iguanid karyotypes. He listed the formula 12 metacentric Macrochromosomes and 24 microchromosomes for the following genera: *Anolis*, *Crotaphytus*, *Dipsosaurus*, and *Phrynosoma*. Hall characterized the genera termed 'sceloporine' . . . as having 12 metacentric Macrochromosomes and a reduced number of microchromosomes, ranging from 10 to 22. Hall's data include members of the genera *Holbrookia*, *Callisaurus*, *Urosaurus*, *Uta* and *Sceloporus*.

Gorman et al. (1967) established that a formula of 12 metacentric macrochromosomes and 24 microchromosomes is primitive among many lizards. They concluded: "Chromosome loss would be of a specialized, advanced character, and this correlates with the phylogenetic position of the sceloporines."

Lowe, Cole, and Patton (1967) proposed that karyotypical evolution can be a matter of Robertsonian fusion, but they did not allow for Robertsonian fission. Cole (1970, 1971a, 1971b) published the karyotypes of the *spinosus* group, the *pyrocephalus* group, and the five monotypic groups (Smith's groups above). He proposed phylogenies of the two polytypic groups and discussed relationships among the others.

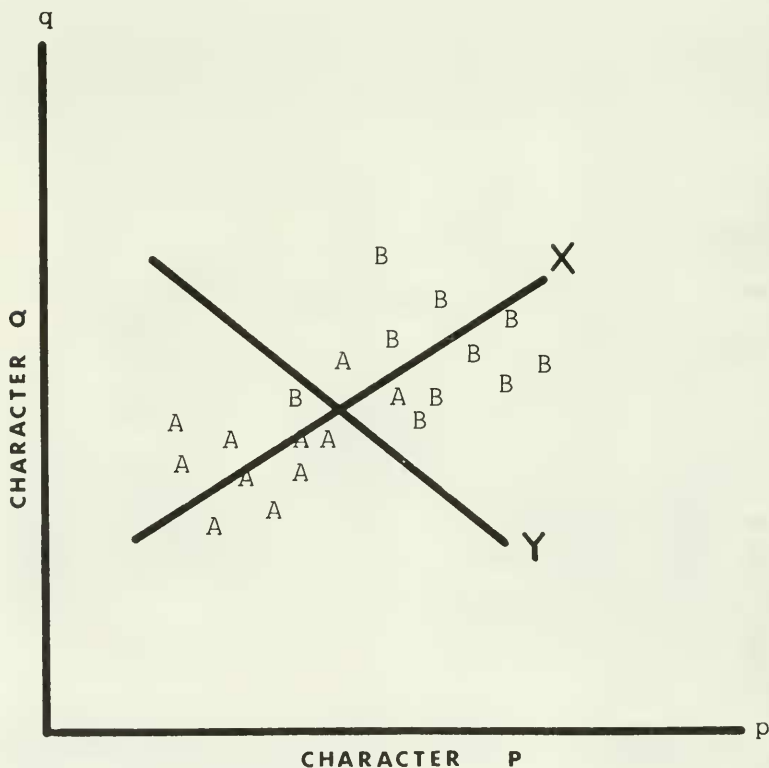
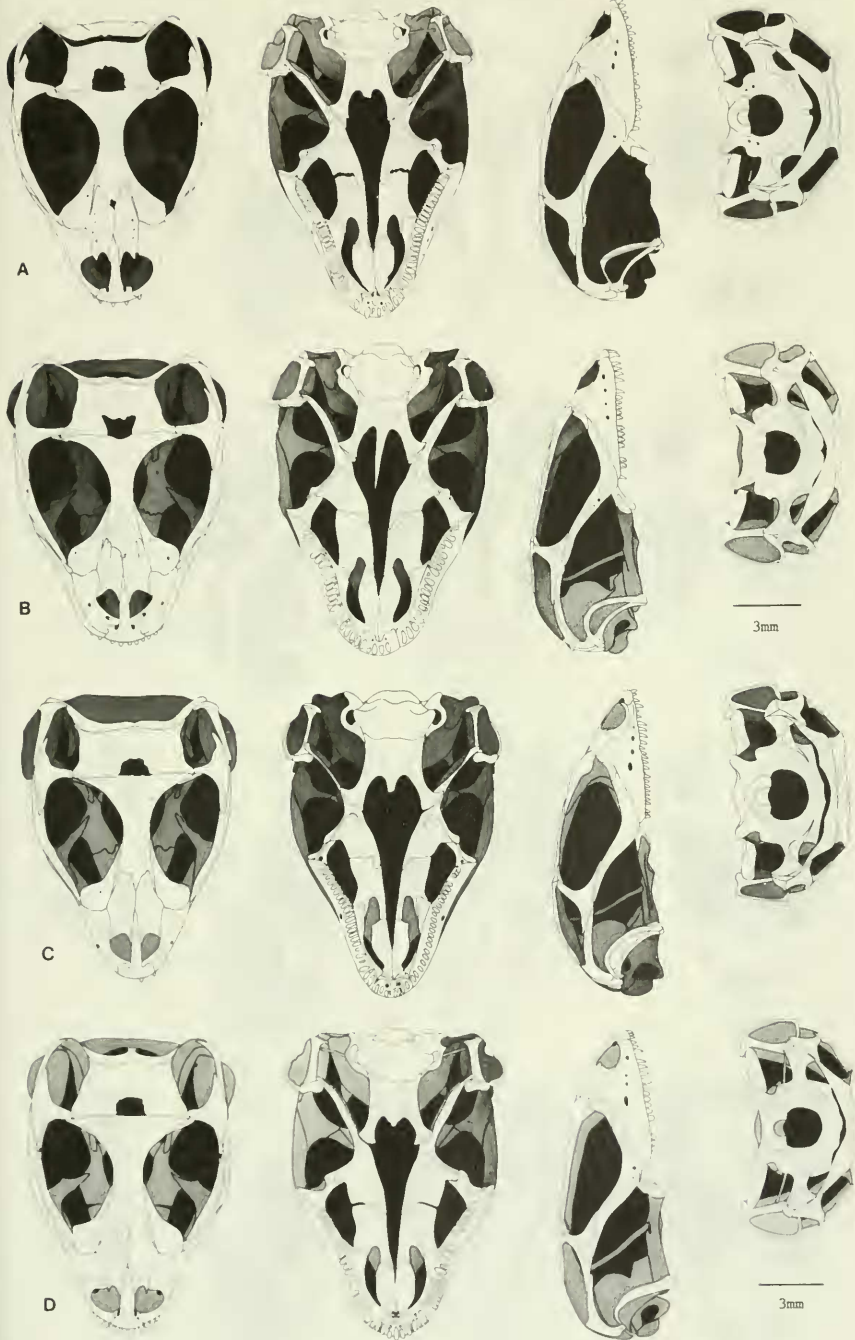
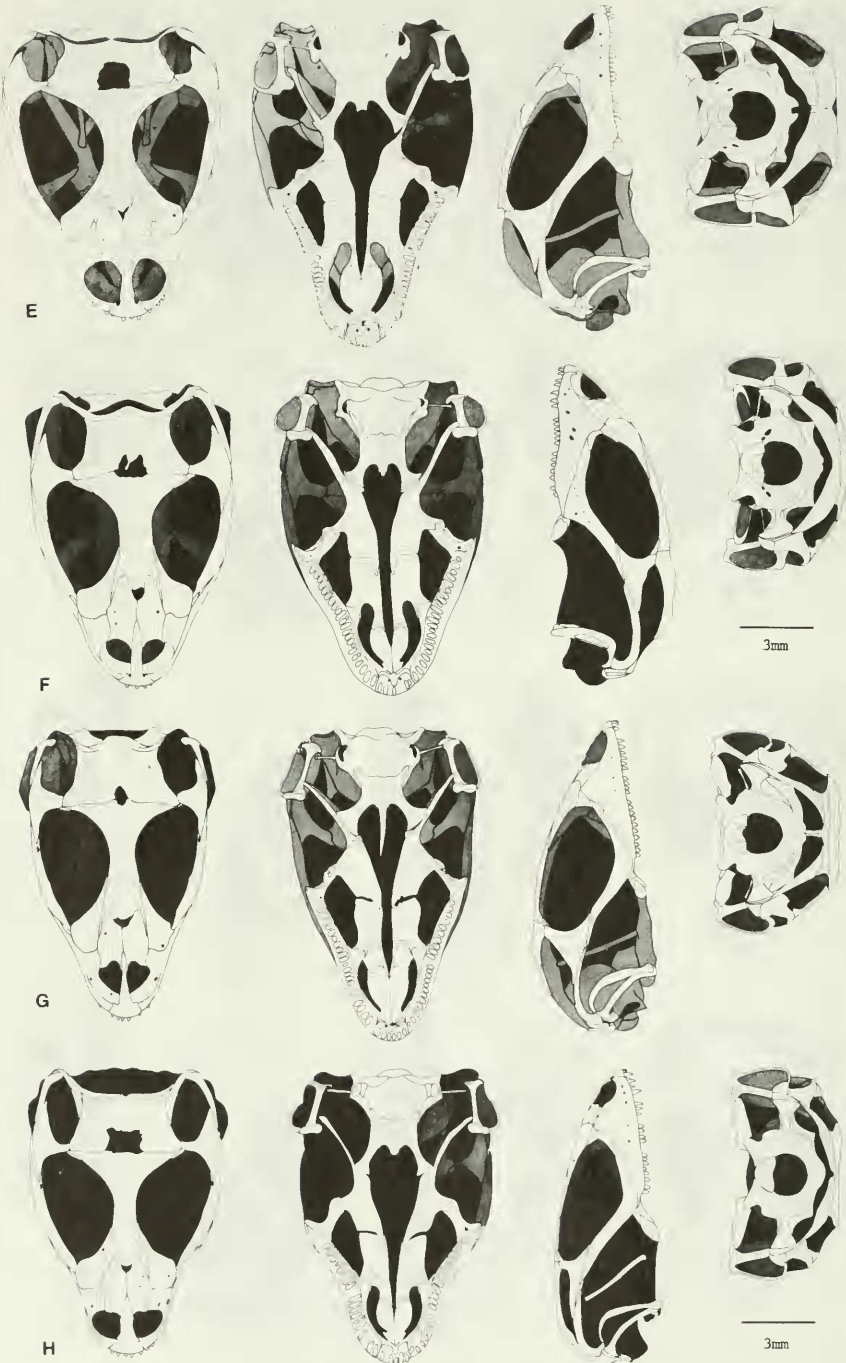


Fig. 9. Theory of canonical analysis.

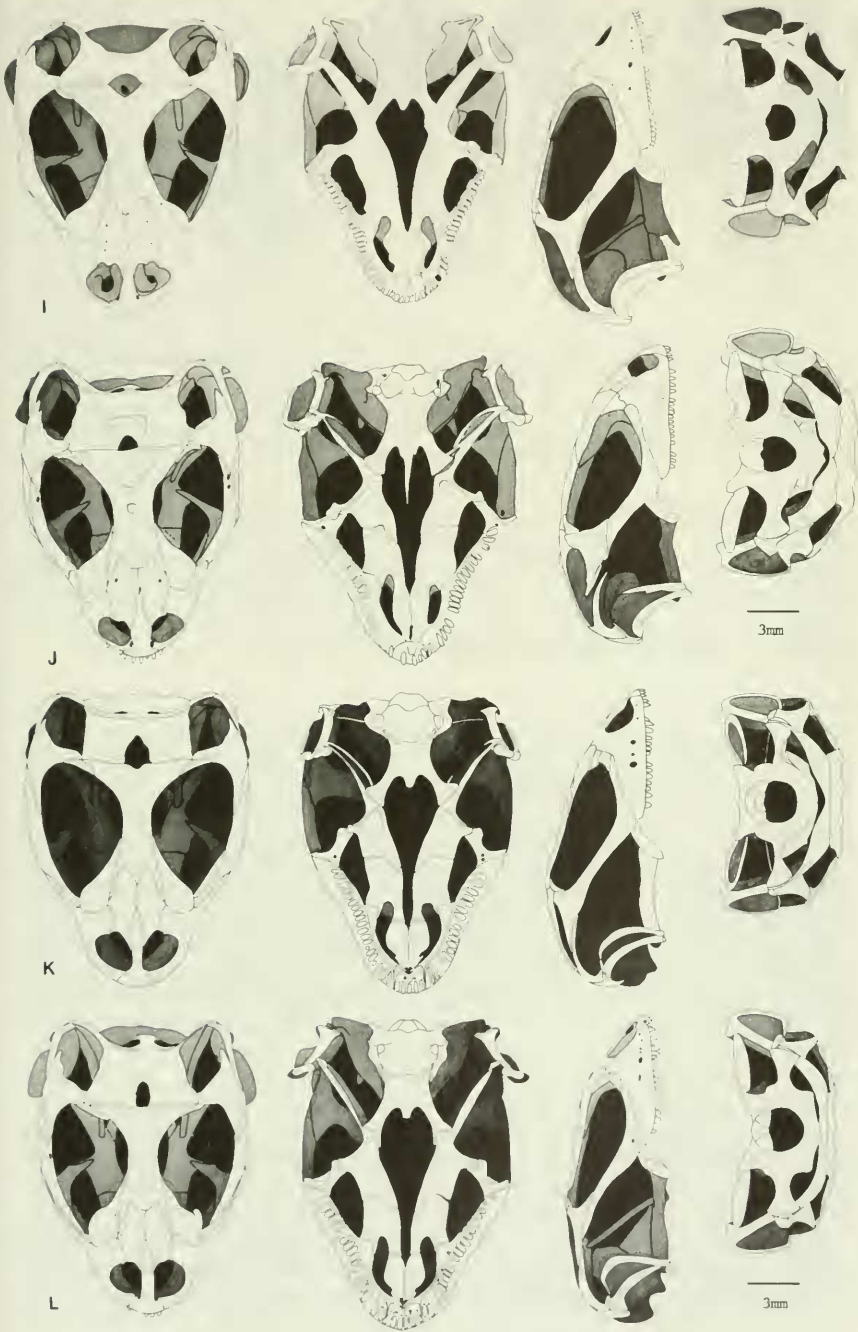
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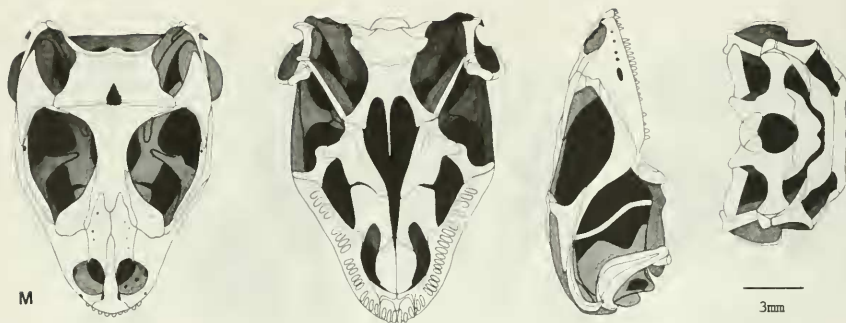


Fig. 10. Dorsal, ventral, lateral, and posterior views of 13 species of *Sceloporus*, representing the major groups within the genus: A, *Sceloporus gadoviae*; B, *S. couchi*; C, *S. maculosus*; D, *S. grammicus microlepidotus*; E, *S. pyrocephalus*; F, *S. scalaris scalaris*; G, *S. siniferus cupreus*; H, *S. variabilis variabilis*; I, *S. spinous caeruleopunctatus*; J, *S. formosus formosus*; K, *S. undulatus elongatus*; L, *S. jarrovi jarrovi*; M, *S. torquatus melanogaster*.

Hall (1970, 1973) has also attempted to establish a phylogeny of *Sceloporus* with major emphasis on karyology. With almost no disagreement concerning the karyotypes of different species, Hall and Cole have produced quite different phylogenies. Hall accepts fission as well as fusion. The occurrence of fission was shown in *Anolis* by Webster, Hall, and Williams (1972).

### Ethology

In 1960 Hunsaker showed that different species of *Sceloporus* have specific display patterns. He showed that females can distinguish between the display patterns of closely related forms. In one part of his study, Hunsaker offered females a choice of males of closely related species. His results show that the females seemed to discern which male was most similar to their own species. This preference by females could be a valid systematic tool. For example, Hunsaker mixed female *jarrovi* with males of *jarrovi*, *dugesii*, and *ornatus*. He found that female *jarrovi* prefer to associate with male *dugesii* over *ornatus* 16 to 11 (61 observations): "These data reflect an apparent tendency of a female *jarrovi* to associate with male *dugesii* more frequently than with a male *ornatus*" (p. 67). Hunsaker also found that female *jarrovi* preferred male *dugesii* over male *jarrovi* 22 to 11 (70 observations) and *ornatus* over *jarrovi* 47 to 12 (47 observations). Possibly the females were not receptive and preferred to avoid their own species. As a result, it may be concluded that *ornatus* is closer to *jarrovi* than is *dugesii* (the *ornatus* males looked more like *jarrovi* to the female *jarrovi* who chose to avoid males). The results do not agree with Smith (1939), and Hunsaker's work is hardly sufficient for systematic conclusions at this point. However, this method may have future prospects.





Fig. 11. Dendrogram generated by external characters (1 to 40).

A more promising aspect of lizard behavior is the analysis of "display action patterns." Carpenter (1962) reported on the display action patterns of *Uta*, *Streptosaurus*, and *Urosaurus* and concluded that *Urosaurus* is a valid genus because its patterns diverge significantly from those of *Uta*.

Purdue and Carpenter (1972a) compared one species of *Petrosaurus*, five species of *Uta*, and five species of *Urosaurus* to 22 species of *Sceloporus*. In their examination of displaying males, they found that the ratio of hip movement to eye movement is a valuable taxonomic character. They have also shown (1972b) that the ratio of shoulder movement to eye movement is a valid species-specific character. Both ratios have been included in our analysis.

### Hematology

Guttman (1970) analyzed the hemoglobin of 12 species of *Sceloporus* using gel electrophoresis. His evidence gives ample support to the proposition that relative movement within the gel is indeed determined by genetic factors. His data also support the arrangement of *cyanogenys* and *torquatus* in one part and *jarrovi* in the other part of a distinct group.

Although some relationships can be shown with electrophoresis, there are problems that make this method suspect. If a heterozygous individual produces two bands, which band is representative of

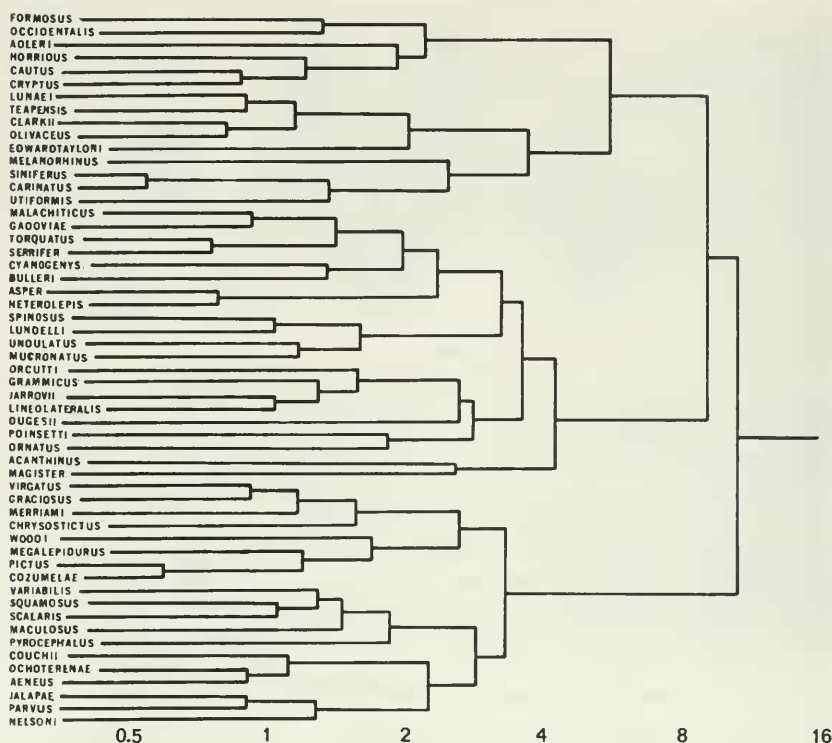


Fig. 12. Dendrogram generated by skull characters (41 to 80).

the position of the species? Sometimes the separation between two bands in a single individual is greater than the distance between single bands of widely divergent species. For example, the total range of relative movement reported by Guttman in the gel is from .11 to .50. *S. undulatus* and *cyanogenys* together cover almost the entire range (.16 to .50). Yet they have a nearly identical band (*cyanogenys* .30; *undulatus* .28 to .33). The relative movement of hemoglobin in an electrophoretic gel is obviously not an indication of degree of relationship. Such a number cannot be used as a numeric character, and the interpretation of electrophoresis must remain subjective and qualitative—which does not rule out its value in systematics. It would be a mistake, however, to consider *variabilis* (.16) and *merriami* (.17) as more closely related than *magister* (.20) and *orcutti* (.41). The members of each pair differ from each other, and further conclusions from electrophoresis may be misleading.

### Temperature

Bogert (1949) computed average body temperatures of 10 forms of *Sceloporus* (Table 1). Two closely related forms (*v. variabilis*

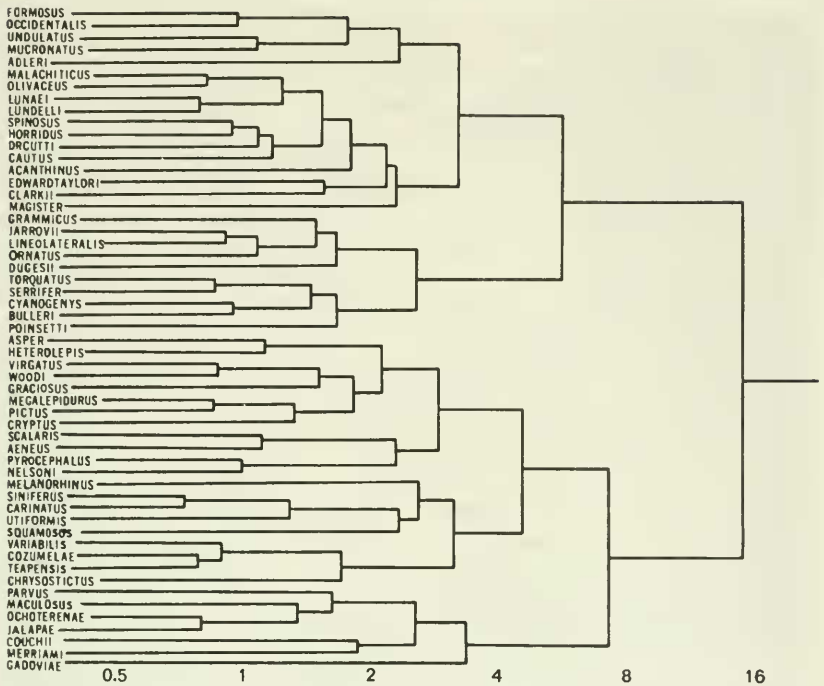


Fig. 13. Dendrogram generated by external and skull characters (1 to 80).

and *v. olloporus*) are separated by 1.4 degrees. However, a span of 1.3 degrees includes five widely divergent species (*magister*, *undulatus*, *poinsetti*, *grammicus*, and *merriami*). In fact, *grammicus* and *merriami* prefer the same temperature. It is doubtful that these data have any systematic value. Further studies, however, may show that temperature preference or optimum temperature for enzyme systems can be useful.

### Paleontology

Brattstrom (1955) reported some thoracic vertebrae, which he identified as *Sceloporus jarrovi*, in Late Pleistocene deposits in Zumpango, Mexico. However, Cole (1970:27) has found that, "The fossil record of *Sceloporus* is practically nonexistent."

### Femoral Pore Secretions

Hunsaker (1960:72) suggested that lizards can identify femoral pore secretions by olfaction or taste:

In *poinsetti* and *cyanogenys* there is a marked disposition of the members of each species to separate when put together. The lizards of one species would establish common territories to the exclusion of the other species. When the secretions of each species were transposed, a reversal of the associative patterns

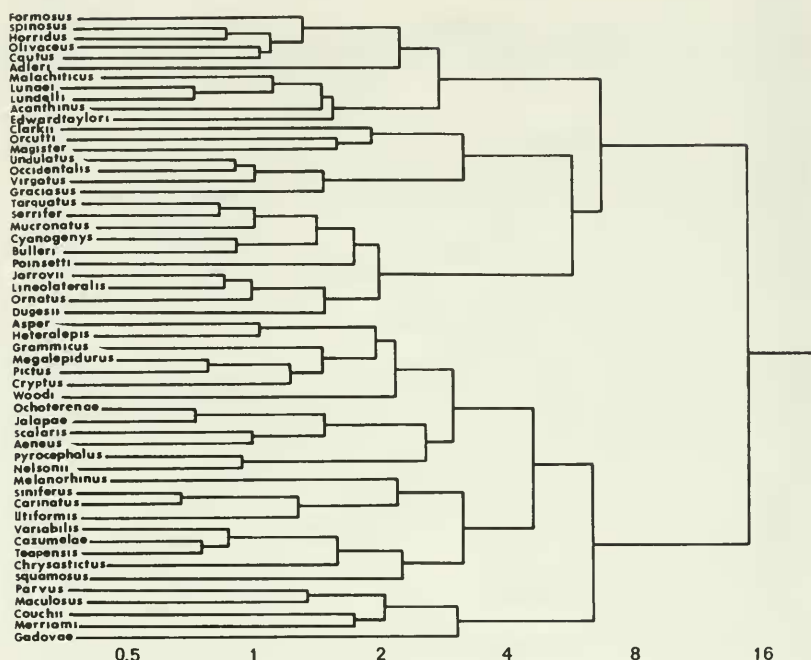


Fig. 14. Dendrogram generated by external, skull, and distribution characters (1 to 82).

occurred, and the members of one species associated with the other and excluded members of their own species.

If femoral pore secretions represent a species-specific territorial marker, then perhaps chemical analysis of these secretions will provide another valuable taxonomic character for future workers.

### Myology

Secoy (1971) examined the myology of eight species of *Sceloporus*, including an extensive examination of *c. clarki*. She concluded that intrageneric myological variation is slight and that speciation in this genus is therefore recent. Although myology may be significant, and even diagnostic, at higher levels or with different taxa, its usefulness within the genus *Sceloporus* must yet be demonstrated.

### MATERIALS AND METHODS

Specimens for this study were acquired from several museum collections and through extensive field collecting by the authors. Most specimens were collected by noosing or shooting with .22 dust shot.

The museum and locality data for specimens from the United States, Mexico, and Central America are as follows: *gadoviae*, BYU 36148 (skull), 45

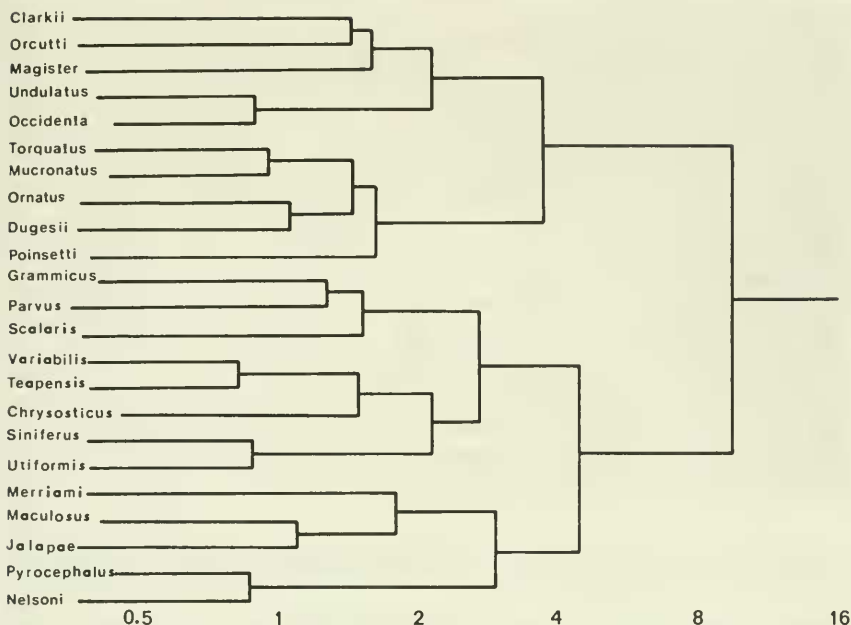


Fig. 15. Dendrogram generated by external, skull, distribution, and display characters (1 to 84).

km S Neuva Italia, Michoacan; *couchi* BYU 36418 (skull), 36417, Huestaca Canon, 18 km W Monterrey, Nuevo Leon; *merriami merriami* BYU 36389 (skull), 13 km S Shumla (Hwy 90 and Pecos River), Val Verde Co., Texas; *parvus scutulatus* BYU 36125 (skull), 4 km N Zimapan, Hidalgo; *parvus parvus* BYU 36126, 36127, 7 km W 3 km N Santiago Anaya, Hidalgo; *jalapae* BYU 36423 (skull) 13 km SE Nochixtlan, Oaxaca, BYU 36422 near Tehuacén (Cacoelepan), Puebla; *ochoteranae* BYU 36004 (skull), 36003, 36005, 36006, Chilpancingo, Guerrero; *maculosus* FMNH 33548 (skull), 32007, 23 km NE Pedricena, Durango; *grammicus microlepidotus* BYU 36300 (skull), 36015, 36017, 36021, Puebla, Puebla, east side of Orizaba, Veracruz; *pictus* BYU 36419 (skull), summit Mt. Acultzingo, Veracruz; *megalepidurus* BYU 36421 (skull), Lake El Chico, Hidalgo, BYU 36094, 36095, 3 km W Limón, Veracruz; *cryptus* AMNH 65835 (skull), Cerro de Humo, Oaxaca; *heterolepis* BYU 36420 (skull), Rancho Primarera, near Guadalajara, Jalisco; *asper* FMNH 32041 (skull), 32043 Uropan, Michoacan; *pyrocephalus* BYU 36268 (skull), 36264, 36265, 36266, 24 km N Colima, Colima; *nelsoni barrancorum* BYU 14316 (skull), 14317, 14318, 14319, 14320, Urique, Chihuahua; *scalaris scalaris* BYU 36132 (skull), Zumpango, Mexico, BYU 36132, Yuridin, Guanajuato, BYU 36133, 2 km S 4 km E Villa Victoria, Mexico; *aeneus aeneus* BYU 36137 (skull), 3 km S Atlacomulco, Mexico, BYU 36136, 4 km S Mexicaltzingo, Mexico, BYU 36138, Salazar, Mexico, BYU 36139, Lagunas Zempoala, Morelos; *siniferus cupreus* BYU 36228 (skull), 36225, 26336, 26229, 74-108 km SE Oaxaca, Oaxaca; *carinatus* BYU 36424 (skull), Rancho Meyapac, Ocozacoatlán, Chiapas; *utiiformis* BYU 36400 (skull), 36401, 36402, 36403, 262 km S Guadalajara (Hwy 80), Jalisco; *squamosus* BYU 36044 (skull), Chinandega Nicaragua; *variabilis variabilis* BYU 36018 (skull), 36163, 36164, 36172, 39 km E Jalapa, Veracruz; *cozumelae* BYU 36428 (skull), 36425, 36426, 36427, 8 km W Progreso, Yucatan; *teapensis* BYU 36121 (skull), 36122, 20 km N Randaes, Chiapas, BYU 36123, Montepio, Veracruz, BYU 36124, Catemaco, Veracruz; *chrysostictus* BYU 36129 (skull), Piste 10 m Yucatan,



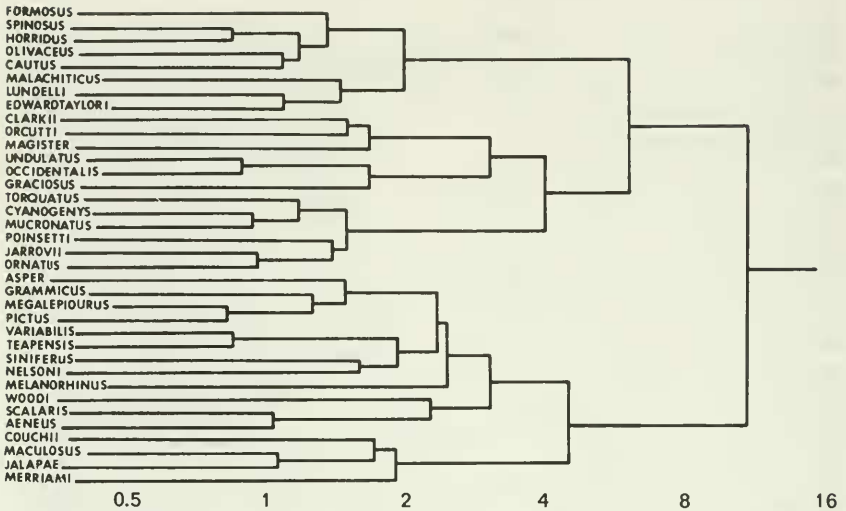


Fig. 16. Dendrogram generated by external. skull, distribution, and chromo-  
some characters (1 to 83).

Yucatan, BYU 36128, Isla mujeres, Quintana Roo; *spinosus caeruleopunctatus* BYU 36213 (skull), 36205, 36212, 36219, 16 km S. Oaxaca, Oaxaca; *orcutti orcutti* BYU 32321 (skull), mountains S of Cabazoh, Riverside Co., California, BYU 30080, 30081, Canyon Guadalupe, Juarez Mountains, Baja California; *clarki clarki* BYU 36056 (skull), 36053, 36054, 36055, San Rafael Trail, Arizona; *melanorhinus calligaster* BYU 14640 (skull), Puerto Vallarta, Jalisco; *magister magister* BYU 8848 (skull), Panoche, San Benito Co., California, BYU 9850, 26 km W Caliente, Lincoln Co., Nevada, BYU 23666, Leeds, Washington Co., Utah, BYU 12886, Hole in the Rock, Kane Co., Utah; *olivaceus* BYU 13048 (skull), Camp Bullis, Texas, BYU 36397, 36398, Laredo, Texas; *cautus* BYU 36250 (skull), 36251, 24 km SE Saltillo, Coahuila; *horridus horridus* BYU 36387 (skull), 36384, Iguala (185 km S Mexico City), Guerrero, BYU 36024, 36025, Chilpancingo, Guerrero, BYU 36231, 132 km S Mexico City Morelos; *edwardtaylori* BYU 36080 (skull), 8 km NW Salina Cruz, Oaxaca; *formosus formosus* BYU 36074 (skull), 36075, 36076, Llano de las Flores, Chiapas; *lundelli lundelli* FMNH 32123 (skull), 32088, 30261, Balchacaj, Campeche; *malachiticus malachiticus* BYU 36032 (skull), 36029, 36030, 36031, Cerro de la Muerte, 95 km S San Jose, Costa Rica; *acanthinus* FMNH 20156 (skull), Tiquisata, Guatemala, FMNH 167111, Santa Clara, Sierra de las Minas, Guatemala, FMNH 10991, Hacienda Chiletta, Sonsonate, El Salvador; *undulatus elongatus* BYU 20642 (skull), 20632, 20633, 20635, Yellow Cat Mining District, Grand Co., Utah; *virgatus* BYU 17031 (skull), 15487, 15488, 17030, 16 km SW San Pedro, Chihuahua; *woodi* BYU 8370 (skull), Englewood, Florida; *occidentalis biseriatus* BYU 30097 (skull), 30094, 23873, 23875, 23878, Rainier Mesa, Nevada Test Site, Mercury, Nye Co., Nevada; *graciosus graciosus* BYU 16700 (skull), 33024, 33049, 21 km NE Provo, Wasatch Co., Utah, BYU 33057, 33058, 5 km E Spanish Fork, Utah Co., Utah; *jarrovi jarrovi* BYU 36007 (skull), 36008, 36010, Huachuca Mountains, Arizona, BYU 36072, Saddle Mountain Trail, Arizona; *lineolateralis* FMNH 100174 (skull), 32030, 10 km NE Pedrecena, Durango; *ornatus caeruleus* BYU 36262 (skull), 36263, 68 km E Torreón, Coahuila; *dugesi dugesi* BYU 36369 (skull), 36342, 36343, 36367, 36370, 165 km S Guadalupe, Jalisco; *torquatus melanogaster* BYU 36309 (skull), 36302, 36303, 36304, 36306, Morelia, Michoacan; *cyanogenys* BYU 36011 (skull), Rancho Santa Anna (13 km SE Padilla), Tamaulipas, BYU

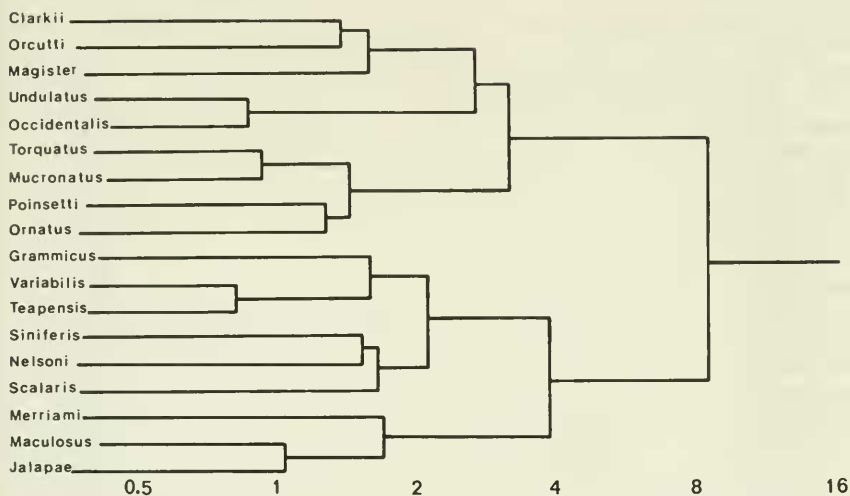


Fig. 17. Dendrogram generated by external, skull, distribution, display, and chromosome characters (1 to 85).

11402, 11404, 11405, Arroyo Vaqueriso, Nuevo Leon; *bulleri* BYU 40082 (skull), 36381, Autlan (185 km S Guadalajara), Jalisco; *maddougalli* FMNH 71661, AM 76119, Isthmus of Tehuantepec, Oaxaca; *mucronatus omiltemanus* BYU 36190 (skull), 36188, 36189, 105 km S Oaxaca, Oaxaca, BYU 36035, Omiltome, Guerrero; *serriifer plioporos* BYU 36182 (skull), 36183, 36149, 36185, 16 km E Jalapa, Veracruz; *poinsetti poinsetti* BYU 13812 (skull), 13814, 13815, 13820, 80 km W Chihuahua City, Chihuahua.

### External Characters

The external characters used were chosen because of their suitability for numerical analysis. Keys and checklists (Smith and Taylor, 1950; Boulenger, 1885; Cope 1900; Van Denburgh, 1922) were examined and all quantitative characteristics were included. Color patterns were omitted because of variations caused by preservatives. The forty external characters utilized are:

- (1) Snout-vent length (mm). (2) Snout-vent/snout-parietal eye. (3) Humerus (from ventral midline to outside of elbow)/snout-vent. (4) Femur (from ventral midline to outside of knee)/snout-vent. (5) Outside length of tibia/snout-parietal eye. (6) Length of fourth toe/femur. (7) Height-to-width ratio of tail at point one head length from vent. (8) Snout-parietal eye (mm). (9) Width of head at parietal eye/snout-parietal-eye. (10) Vertical height of head at parietal eye/snout-parietal eye. (11) Width of head anterior to orbit/snout-parietal eye. (12) Distance between nares/snout-parietal eye. (13) Length of frontal scale(s)/snout-parietal eye. (14) Length of frontal scale(s)/snout-parietal eye. (14) Length of frontal scale(s)/smallest width of frontal. (15) Largest linear measurement on internasal scale/snout-parietal eye. (16) Length of interparietal/width of same (through parietal eye). (17) Width of widest supraocular/snout-parietal eye. (18) Width of widest supraocular/length of same. (19) Parietal eye to posterior edge of interparietal/length of interparietal. (20) Length of median frontonasal/width of same. (21) Length of median frontonasal/snout-parietal eye. (22) Dorsals from interparietal to posterior margin of thigh. (24) Dorsals equal to

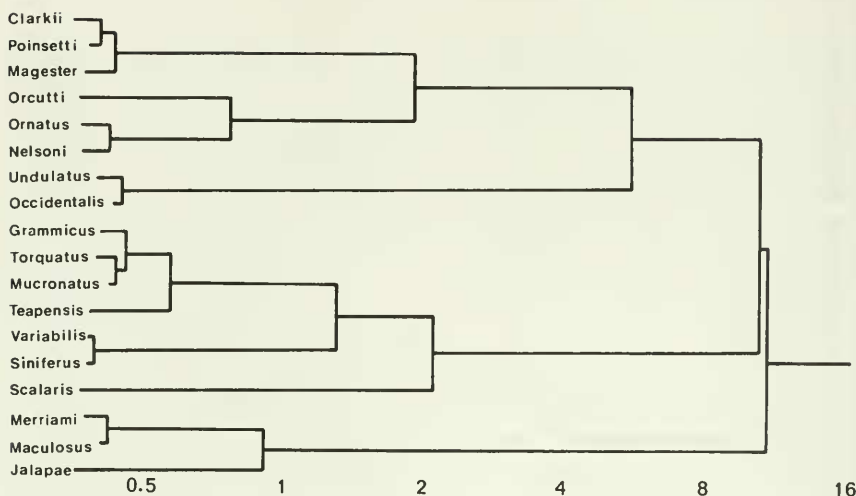


Fig. 18. Dendrogram generated by distribution, display, and chromosome characters (81 to 85).

one head length (between points 2 and 3 head lengths posterior to interparietal). (25) Laterals equal to one head length midway between limbs. (26) Ventrals equal to one head length (between points 2 and 3 head lengths posterior of snout). (27) Dorsals equal to  $\frac{1}{2}$  head length (counting laterally from midline at a point 2 head lengths from interparietal). (28) Ventrals equal to  $\frac{1}{2}$  head length (counting laterally from midline at a point 3 head lengths from snout). (29) Total femoral pores (both sides). (30) Ventrals between medial limits of femoral pores. (31) Ventrals from vent to a line connecting femoral pore series. (32) Caudals equal to one head length (between points 1 and 2 head lengths from vent). (33) Supralabials (total both sides and rostral). (34) Infralabials (total both sides and mental). (35) Sublabials (total both sides and mental). (36) Caudals around tail one head length from vent. (37) Dorsals equal to one interparietal (counting posterior from interparietal). (38) Ventrals equal to one interparietal (counting anterior from vent). (39) Head shields in contact with interparietal. (40) Fourth toe lamellae.

### Skulls

*Preparation.* Skulls were prepared by boiling 15-20 minutes in 50 ml water with a few drops of detergent and  $\text{NH}_4\text{OH}$ . After boiling, they were allowed to dry until the muscles were easily removed with forceps. This procedure was repeated several times and the last remains of muscle were removed by dipping the skull in Clorox bleach.

*Whitening of skulls.* Kier, Grant, and Yochelson (1965:453-56) described a technique widely used in paleontological preparations but possibly new to investigators of herpetological osteology. The skull was first blackened by dipping in ink. (Shafer's permanent blue-black is excellent because it stains the skulls effectively and is easily removed by dipping the skull in a mild solution of  $\text{NH}_4\text{OH}$ .) The blackened skull was then highlighted with a thin layer of  $\text{NH}_4\text{Cl}$ . The dry  $\text{NH}_4\text{Cl}$  was placed in the chamber of a

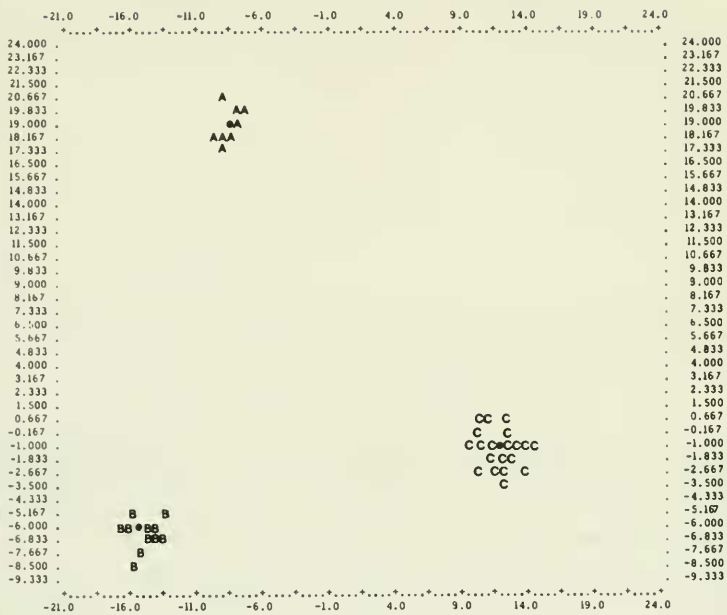


Fig. 19. Canonical display of three groups: I(A), II(B), and III(C).

100 ml pipette, and the open end of the pipette was attached with rubber tubing to a squeeze bulb. To vaporize the  $\text{NH}_4\text{Cl}$ , the pipette was heated over a flame. With careful pressure on the squeeze bulb, the skull was then highlighted with  $\text{NH}_4\text{Cl}$  vapor. This technique enhances the suture lines in black contrast and facilitates the study of photographs.

*Skull photography.* Several workers have taken measurements directly from skulls with calipers (Weiner and Smith, 1965; Jenkins and Tanner, 1968; Avery and Tanner, 1971). However, the small size of some species makes it virtually impossible to take precise measurements directly from the skulls. Weiner and Smith (1965) made some of their skull measurements with the aid of an ocular micrometer and a microscope. But measurements through a microscope or on a photograph are subject to error caused by variation in angle of view. Such measurements would be acceptable, however, if the angle of view were kept constant. Lewis (1944) studied the determination of dress patterns from photographs and found that if the subjects were properly oriented, correct three-dimensional dress patterns could be determined. To minimize the problem of distortion and provide constant orientation of skulls, special equipment was constructed. The apparatus (Fig. 1) was constructed to minimize variations in angle of view. This structure consists of a circular outer platform that can be leveled with spirit levels. The skull is placed on a second platform in the center. The inner plat-

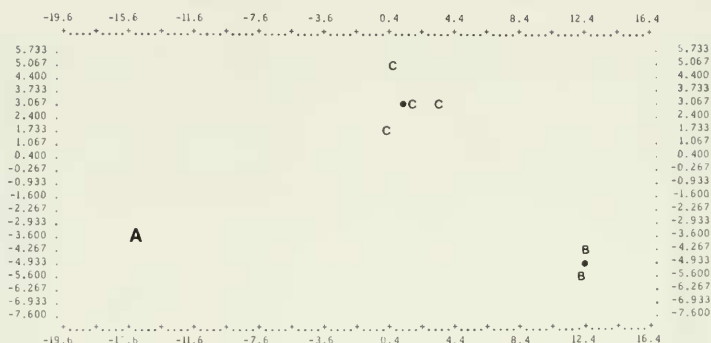


Fig. 20. Canonical display of the three subgroups of group I.

form can be tilted along two planes as well as adjusted vertically until specific reference lines on the skull are parallel with the outside platform. A camera (Nikon FTN with Kodak plus X film) was placed over the skull with spirit levels attached to the camera back so that the reference lines through the skull and the film in the camera were always as nearly parallel as possible.

A line through the tip of the premaxilla and the center of the foramen magnum was the first reference for dorsal, ventral, and lateral views. The second reference line for the dorsal view passed through the anterolateral corners of the parietals. The second reference line for the ventral view passed through the lateral tips of the ectopterygoids. The second reference line for the lateral view was the surface of the frontoparietal suture, which was oriented at right angles to the outer platform. The posterior view was arranged so that the surface of the parietal bone was at right angles to the outer platform and a line through the lateral tips of the exoccipitals was parallel to the outer platform.

Further to minimize possible error caused by variation in angle of view, all skull measurements were converted to ratios between two distances measured in the same direction on the same photograph. Although this technique reduces the effects of distortion, it unfortunately eliminates most of the traditional skull characters (width and length ratios of skull members).

Illustrations were prepared by projecting and tracing the photographs with a Saltzman Projector. Detail was added to the tracings with the aid of a binocular microscope (Presch, 1969; Nash and Tanner, 1970).

### Skull Characters

The following 40 characters (numbers 41-80) were computed for each skull:

(41) Posterior extent of supraoccipital on midline to anterior border of parietal foramen/parietal foramen to suture between nasals (Fig. 2). (42) Length of suture between nasals/parietal foramen to suture between nasals (Fig. 2). (43)



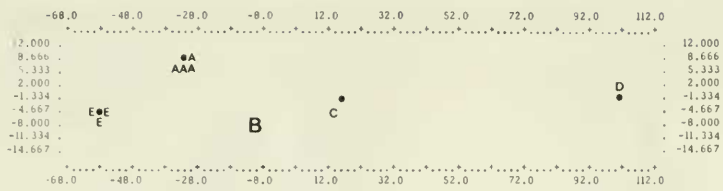


Fig. 21. Canonical display of the five subgroups of group II.

Length of premaxilla/parietal foramen to suture between nasals (Fig. 2). (44) Posterior tip of suture between frontal and nasal to posterior end of suture between prefrontal and nasal/posterior end of suture between prefrontal and nasal to anterior end of suture between prefrontal and nasal (Fig. 2). (45) Anterior end of suture between prefrontal and nasal to anterior end of suture between maxillary and nasal/parietal foramen to suture between nasals (Fig. 2). (46) Anterior end of suture between maxillary and nasal to anterior end of suture between maxillary and premaxillary/parietal foramen to suture between nasals (Fig. 2). (47) Pineal foramen to posterior end of suture between prefrontal and lacrimal/parietal foramen to suture between nasals (Fig. 2). (48) Posterior extent of lateral wing of parietal to posterior end of suture between parietal and postorbital/posterior extent of supraoccipital on midline to anterior border of parietal foramen (Fig. 2). (49) Length of postorbital/posterior end of suture between parietal and postorbital to anterior edge of parietal foramen (Fig. 2). (50) Posterior tip of prefrontal to anterior end of suture between prefrontal and nasal/posterior end of suture between prefrontal and lachrymal to anterior tip of prefrontal (Fig. 2). (51) Most narrow width of frontal/anterior width of parietal (along suture with postorbital) (Fig. 3). (52) Lateral side of jugal on transverse line through anterior border of parietal foramen to lateral extent of suture between postorbital and parietal/anterior width of parietal (Fig. 3). (53) Interfenestral width (on line passing through posterior tips of both postorbitals)/anterior width of parietal (Fig. 3). (54) Lateral edge of parietal on line passing through posterior tips of both postorbitals to posterior tip of postorbital on same side/anterior width of parietal (Fig. 3). (55) Anterior end of suture between prefrontal and nasal to posterior end of suture between prefrontal and lacrimal distance between left and right anterior ends of suture between prefrontal and nasal (Fig. 3). (56) Internarial width/distance between left and right anterior ends of suture between maxillary and premaxillary (Fig. 3). (57) Posterior tip of occipital condyle to medial corner of tip of basiptyergoid process of the basisphenoid/lateral tip of ectopterygoid to anterior tip of premaxilla (Fig. 4). (58) Medial corner of tip of basiptyergoid process to lateral tip of ectopterygoid/lateral tip of ectopterygoid to anterior tip of premaxilla (Fig. 4). (59) Posterior corner of lateral side of palatine to lateral limit of suture between palatine and maxilla/lateral tip of ectopterygoid to anterior tip of premaxilla (Fig. 4). (60) Posterior

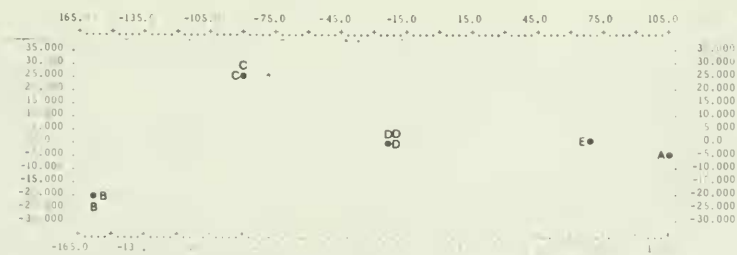


Fig. 22. Canonical display of the five subgroups of group III.

TABLE 1. Average body temperature of some *Sceloporus* as reported by Bogert (1949).

Temperature C	Species
36.9	<i>variabilis variabilis</i>
36.2	<i>woodi</i>
35.4	<i>variabilis olloporus</i>
35.3	<i>squamosus</i>
34.9	<i>magister</i>
34.8	<i>undulatus consobrinus</i>
34.2	<i>poinsetti</i>
33.6	<i>grammicus disparilis</i>
33.6	<i>merriami</i>
32.9	<i>formosus malachiticus</i>

tip of quadrate ramus of pterygoid to lateral tip of ectopterygoid/lateral tip of ectopterygoid to anterior tip of premaxilla (Fig. 4). (61) Lateral tip of ectopterygoid to medial limit of suture between maxilla and ectopterygoid/distance between lateral tips of ectopterygoid (Fig. 5). (62) Medial limit of suture between maxilla and ectopterygoid to posterior corner of lateral side of palatine/distance between lateral tips of the ectopterygoid (Fig. 5). (63) Posterior corner of lateral side of palatine to medial limit of suture between palatine and pterygoid/distance between lateral tips of ectopterygoids (Fig. 5). (64) Smallest width of basisphenoid/distance between lateral tips of ectopterygoids (Fig. 5). (65) Diagonal distance from lateral tip of ectopterygoid on one side to posterior tip of quadrate ramus of pterygoid on other side/length between the same points on one side (Fig. 5). (66) Five times the tangent of the angle between the midline and the extended line that passes through the midpoint on the tip of the basiptyergoid process and the midpoint on the most narrow part of the neck of the basiptyergoid process (Fig. 5). (67) Tip of premaxilla to most ventral extent of ectopterygoid projected onto a line from the tip of premaxilla to tip of quadrate ramus of pterygoid/tip of premaxilla to posterior tip of postorbital (Fig. 6). (68) Most ventral extent of ectopterygoid to tip of quadrate ramus of pterygoid projected onto a line from the tip of premaxilla to tip of quadrate ramus of pterygoid/tip of premaxilla to posterior tip of postorbital (Fig. 6). (69) Tip of premaxilla to anterior end of suture between prefrontal and lacrimal (parallel to denominator)/tip of premaxilla to posterior tip of postorbital (Fig. 6). (70) Anterior end of suture between prefrontal and lacrimal to posterior tip of prefrontal (parallel with denominator)/tip of premaxilla to posterior tip of postorbital (Fig. 6). (71) Posterior tip of prefrontal to anterior end of suture between postfrontal and parietal (parallel with denominator)/tip of premaxilla to posterior tip of postorbital (Fig. 6). (72) Anterior end of suture between prefrontal and lacrimal to posterior tip of prefrontal (direct)/same as numerator projected onto the line between the tip of the premaxilla and the posterior tip of postorbital (Fig. 6). (73) Posterior tip of prefrontal to most ventral extent of ectopterygoid/anterior end of suture between postfrontal and parietal to tip of quadrate ramus of pterygoid (Fig. 6). (74) Dorsal ridge of supraoccipital to dorsal edge of foramen magnum/top of parietal at midline (passes vertically through medial ridge of supraoccipital and through center of occipital condyle) to ventral edge of parietal at midline (Fig. 7). (75) Height of foramen magnum along midline/top of parietal to ventral edge of parietal (Fig. 7). (76) Ventral edge of foramen magnum on midline to ventral edge of condyle/dorsal-ventral height of parietal (Fig. 7). (77) Dorsal corner of lateral process of exoccipital to ventral corner of lateral process of exoccipital/dorsal-ventral height of parietal (Fig. 7). (78) Distance between right and left dorsal corners of lateral process of exoccipital/distance between right and left ventral corners of basioccipital tubercles (Fig. 7). (79) Five times the tangent of the angle formed by the dorsal corner of the lateral process of the exoccipital and its intersection with the midline (at right angles) and the ventral corner of the basioccipital tubercle (all points on one side) (Fig. 7). (80) Five times the tangent of the angle formed

TABLE 2. Groups and subgroups in the genus *Sceloporus*.

Group I	Group II	Group III
Subgroup A <i>gadoviae</i>	Subgroup A <i>grammicus</i> <i>pictus</i> <i>megalepidurus</i> <i>cryptus</i> <i>shannonorum</i> * <i>heterolepis</i> <i>asper</i>	Subgroup A <i>spinosus</i> <i>orcutti</i> <i>clarki</i> <i>melanorhinus</i> <i>magister</i> <i>olivaceus</i> <i>cautus</i> <i>horridus</i> <i>edwardtaylori</i>
Subgroup B <i>couchi</i> <i>merriami</i>	Subgroup B <i>pyrocephalus</i> <i>nelsoni</i>	Subgroup B <i>formosus</i> <i>lunaei</i> <i>malachiticus</i> <i>acanthinus</i>
Subgroup C <i>maculosus</i> <i>parvus</i> <i>jalapae</i> <i>ochoterenae</i>	Subgroup C <i>scalaris</i> <i>goldmani</i> * <i>aeneus</i>	Subgroup C <i>undulatus</i> <i>virgatus</i> <i>woodi</i> <i>occidentalis</i> <i>graciosus</i>
	Subgroup D <i>siniferus</i> <i>carinatus</i> <i>utiformis</i> <i>squamosus</i>	Subgroup D <i>jarrovi</i> <i>lineolateralis</i> <i>ornatus</i> <i>dugesi</i>
	Subgroup E <i>variabilis</i> <i>cozumelae</i> <i>teapensis</i> <i>chrysostictus</i>	Subgroup E <i>torquatus</i> <i>cyanogenys</i> <i>bulleri</i> <i>insignis</i> * <i>macdougalli</i> <i>mucronatus</i> <i>serrifer</i> <i>poinsetti</i>

\*Species not examined in this study.

by the shortest width of the parietal, its intersection with the midline, and the line from that intersection to the dorsal corner of the lateral process of the exoccipital (all points on one side) (Fig. 7).

### Other Characters

**Karyology.** Extensive karyological data are available for most species of *Sceloporus* (see Literature Review—Karyology). Although many characters can be described for each species, the only karyological character included in this study is the number of microchromosomes. A change in microchromosomal number is theoretically a single karyotic event, and such events may indicate relationships. Hopefully, additional characters will soon be available for numeric analysis.

**Display-action patterns.** Although display-action patterns involve a complex of activities, only two measurements were con-

sidered: the ratio of vertical movement of the shoulder to the vertical movement of the eye and the ratio of vertical movement of the hip to the vertical movement of the eye (Purdue and Carpenter, 1972b).

*Zoogeography.* The approximate latitude and longitude of the center of distribution for each species were included as additional characters. Of course, a simple measure of latitude and longitude does not allow for altitude, climate, habitat preference, or natural barriers such as mountains and rivers. However, differences in latitude and longitude are a measurement of horizontal distance and represent a crude measure of natural resistance to gene flow. Latitude is also somewhat correlated with climatic gradients.

### Data Analysis

*Justification.* Hennig (1966:74) defined species relationships as follows: "A species 'x' is more closely related to another species 'y' than it is to a third species 'z' if and only if it has at least one stem species in common with species 'y' that is not also a stem species of 'z'." Hennig proposed that classification be based on phylogenetic kinship and not form similarity because frogs and tadpoles should not be different taxa. Bigelow (1958) said that the measure of phylogenetic relationship is the "relative recency of common ancestry." These definitions of relationship seem to be circular. Phylogenies are based on circumstantial evidence, so it is impossible for Hennig to prove whether or not "x" and "y" have a stem species that is not an ancestor of "z." We believe that phylogenetic relationships are manufactured in the mind of the taxonomist from phenetic data and form similarities. We therefore reject Hennig's and Bigelow's proposals and suggest that the best phenotypic dendrogram (containing representatives of all populations of the group under consideration and including a sufficient number of characters manipulated in the best numeric manner) is also the best source for the most probable phylogeny. Sokal and Sneath (1963) suggested that at least 60 characters are necessary for highly significant results. Our study has

TABLE 4. Means and standard deviations for the eight diagnostic characters in groups I, II, and III.

Character	Groups					
	Group I		Group II		Group III	
	Mean	S.D.	Mean	S.D.	Mean	S.D.
32	13.97	1.00	9.90	1.55	7.90	0.72
7	10.02	0.88	10.98	1.23	9.45	0.63
27	9.08	1.72	6.59	1.65	4.39	1.03
13	4.05	0.17	3.84	0.22	3.71	0.21
30	4.71	4.55	9.49	5.64	9.04	3.06
6	10.15	3.01	10.93	1.14	9.32	1.00
39	7.19	1.94	7.48	1.57	5.70	1.04
70	2.56	0.19	2.34	0.24	2.55	0.19

TABLE 3. Results of stepwise discriminate analysis of the three groups.

Step	Variable Added	Group I	Group II	Group III	Percent Correctly Identified	F-Ratio This Variable	Degrees of Freedom	Approximate F-Value (U-statistic)	Degrees of Freedom
1	32	8	10	26	80	98.3	2, 52	98.3	2, 52
2	7	8	13	28	89	13.4	2, 51	43.3	4, 102
3	27	8	15	28	93	7.75	2, 50	34.9	6, 100
4	13	8	17	28	96	7.55	2, 49	31.1	8, 98
5	30	8	18	28	98	7.17	2, 48	29.1	10, 96
6	6	8	18	28	98	7.81	2, 47	28.6	12, 94
7	39	8	18	28	98	6.04	2, 46	27.8	14, 92
8	70	8	18	29	100	6.38	2, 45	27.7	16, 90

TABLE 5. Results of stepwise discriminate analysis of the three subgroups of Group I.

Step	Variable Added	Part A	Part B	Part C	Percent Correctly Identified	F-Ratio This Variable	Degrees of Freedom	Approximate F-Value (U-statistic)	Degrees of Freedom
1	7	2	1	5	89	86.62	2, 6	86.6	2, 6
2	23	2	2	5	100	51.71	2, 5	61.1	4, 10

TABLE 6. Means and standard deviations of the two diagnostic characters in the three subgroups of Group I.

Character	Parts					
	Part A		Part B		Part C	
	Mean	S.D.	Mean	S.D.	Mean	S.D.
7	12.04	0.00	9.33	0.48	9.90	0.13
23	81.00	0.00	75.00	5.66	55.43	2.67



TABLE 7. Results of stepwise discriminate analysis of the five subgroups of group II.

Step	Variable Added	Part A	Part B	Part C	Part D	Part E	Percent Correctly Identified	F-Ratio This Variable	Degrees of Freedom	Approximate F-Value (U-statistic)	Degrees of Freedom
1	17	5	1	2	3	2	72	24.4	4, 13	24.38	4, 13
2	40	5	2	2	3	4	89	11.9	4, 12	16.49	8, 24
3	7	5	2	2	4	4	94	6.3	4, 11	13.39	12, 29
4	64	6	2	2	4	4	100	6.9	4, 10	13.21	16, 31
5	21	5	2	2	4	4	94	6.5	4, 9	13.82	20, 30
6	75	5	2	2	4	4	94	6.4	4, 8	15.14	24, 29
7	20	6	2	2	4	4	100	7.3	4, 7	17.69	28, 26

TABLE 8. Means and standard deviations of the seven diagnostic characters in the five subgroups of Group II.

Character	Parts									
	Part A		Part B		Part C		Part D		Part E	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
17	1.57	0.12	2.23	0.04	1.38	0.02	2.01	0.23	2.23	0.08
40	21.13	1.36	16.75	0.71	19.04	0.41	23.06	1.48	21.94	0.63
7	10.48	0.34	13.72	1.36	10.45	0.49	11.45	0.79	10.18	0.53
64	23.22	2.14	23.00	3.84	23.80	0.95	23.61	2.13	24.19	1.76
21	1.91	0.19	1.73	0.01	1.55	0.01	1.52	0.19	1.40	0.17
75	4.83	0.33	5.37	0.16	4.87	0.17	4.85	0.44	4.80	0.27

TABLE 9. Stepwise discriminate analysis of Group II. Number of pairs separated at .95, .99, and .999 confidence levels for each step.

Step	Confidence Level		
	.95	.99	.999
1	7	6	6
2	9	8	7
3	9	8	8
4	9	8	8
5	8	8	8
6	8	8	8
7	8	8	8
8	9	8	8
9	9	9	8
10	10	10	9
11	10	10	10
12	10	10	8
13	10	8	8

utilized over 80 characters with the hope that at least 60 are significantly independent.

*Cluster analysis.* All past statistical studies of this genus have utilized some form of univariate analysis (except Lundelius, 1957, who considered only two species). That is, relationships were determined by combining the indications presented by each individual character. The problems with univariate analysis and the advantages of multivariate analysis were discussed at length by Ingram and Tanner (1971). They stated (pp. 25-26):

Another more compelling reason for using multivariate analysis of data concerns what is actually being analyzed. Taxonomists are classifying whole organisms, not any one scale count (Mayr, 1969; Sokal and Sneath, 1963). Univariate methods consider only one variable at a time as completely unrelated to all other variables. Multivariate methods consider groups of characters, as a unit, and their relationships with each other. This is a better approximation of the organisms with which taxonomists are concerned.

The arrangement of species into phenetic clusters was accomplished with Ward's Cluster Analysis. This procedure was used because (1) it is available as a packaged computer program (Wishart, 1968), (2) it has been used with success by other workers in herpetological systematics (Ingram and Tanner, 1971; Smith and Tanner 1974), (3) it is theoretically sound, and (4) it produces satisfactory results.

Ingram and Tanner (1971:26) explained the theory of Ward's Cluster Analysis:

*Cluster Analysis.* When a taxonomic study is made taking two measurements on each individual, the specimens studied could be represented as points on a two-dimensional space. The resulting graph would illustrate the phenotypic interrelations of the individuals. Expanding this to 90 measurements on each individual, the specimens could be represented as points in a hypothetical 90 (or p)-dimensional hyperspace. The representation of individuals on a 90-dimensional graph is best grasped by visualizing many points in space grouped in clusters of varying size. The number of dimensions in the hyperspace is equal to the number of variables measured. This concept of individuals being repre-

TABLE 10. Results of stepwise discriminate analysis of the five subgroups of group III.

Step	Variable Added	Part A	Part B	Part C	Part D	Part E	Percent Correctly Identified	F-Ratio This Variable	Degrees of Freedom	Approximate F-Value (U-statistic)	Degrees of Freedom
1	31	6	3	2	0	3	48	19.02	4, 24	19.02	4, 24
2	81	8	4	5	1	4	76	11.16	4, 23	14.38	8, 46
3	24	8	4	5	4	6	93	9.61	4, 22	13.5	12, 58
4	7	8	5	5	4	6	97	7.31	4, 21	12.99	16, 64
5	37	8	5	5	4	6	97	5.47	4, 20	12.42	20, 67
6	61	9	5	5	4	6	100	5.25	4, 19	12.33	24, 67

TABLE 11. Means and standard deviations of the six diagnostic characters used to classify the five subgroups of group III.

Character	Parts									
	Part A		Part B		Part C		Part D		Part E	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
31	4.76	0.68	5.38	0.54	6.85	0.76	7.63	1.20	7.67	0.74
81	24.14	6.58	15.50	3.84	34.60	5.18	24.75	3.40	22.50	5.17
24	6.15	1.20	7.55	0.83	9.35	1.11	10.25	0.98	6.65	1.33
7	9.39	0.46	10.16	0.41	9.58	0.27	8.51	0.42	9.47	0.55
37	3.71	0.80	3.98	0.70	5.53	0.36	4.60	0.75	3.67	0.38
61	14.55	1.43	16.41	0.87	14.92	1.37	14.00	0.89	14.55	1.38

TABLE 12. Stepwise discriminate analysis of group III. Number of pairs separated at .95, .99 and .999 confidence levels for each step.

Step	Confidence Level		
	.95	.99	.999
1	6	6	5
2	9	9	8
3	10	10	8
4	10	10	9
5	10	10	8
6	10	10	10
7	10	10	10
8	10	10	9
9	10	10	99
10	10	10	9

sented as points in a p-dimensional space is essential to cluster and discriminant analyses.

Ward's method of cluster analysis forms spherical clusters of individuals in the hyperspace. New clusters are formed by measuring the distance from each individual in the original cluster to the center of the cluster, called the centroid. These distances are summed to form the error sum of squares for the cluster. The individuals to be added to the cluster are conditionally added, and the new centroid formed. An error sum of squares for the newly formed cluster is calculated. This procedure is done for all possible entries to the original cluster (possible entries include other clusters as well as individuals). The entry that causes the least increase in the error sum of squares is joined to the original cluster. Each new cluster is formed by joining those individuals that move the centroid the smallest distance. In other words, each cluster is composed of those individuals located closest to each other in the hyperspace. Thus, it is seen that this method unites individuals of the highest morphological similarity first (Wishart, 1969).

Besides producing a phenetic dendrogram, Wishart's program (1968) provides other useful information, including (1) raw-data listing (numeric and binary), (2) maxima and minima for numeric data, (3) standard scores for numeric data, (4) means and standard deviations, (5) product-moment correlation coefficients, (6) principle components eigenvalues, (7) percentage and cumulative variances, (8) eigenvectors, (9) binary attribute frequencies, (10) binary attribute percentage occurrences, (11) similarity matrix, (12) "normalized" classification array, (13) listing of sample numbers for each cluster, (14) cluster means, standard deviations, F-ratios and T-values for continuous variable in each cluster, (15) cluster frequencies for binary attributes, (16) cluster percentage occurrences for binary attributes, (17) binary attribute percentage ratios.

The F-ratios printed for each character in each cluster are computed as the variation within that cluster divided by the variation in the total population. It must be remembered that this is not the traditional F-ratio (variance within clusters/variance between clusters). A character with a low F-ratio in one cluster is not necessarily a diagnostic character. The high total variance may be caused by variance within another cluster rather than variance between clus-

TABLE 13. X and Y canonical coordinates of the species in groups I, II, and III.

Species	X	Y	Species	X	Y
Group I			Group III		
<i>gadoviae</i>	-8.8	18.4	<i>spinosus</i>	12.5	-1.7
<i>merriami</i>	-7.8	19.6	<i>edwardtaylori</i>	11.9	-1.8
<i>couchi</i>	-8.5	18.1	<i>melanorhinus</i>	10.1	-0.4
<i>parvus</i>	-7.7	20.1	<i>clarki</i>	12.7	-1.1
<i>maculosus</i>	-8.2	18.7	<i>orcutti</i>	13.7	-0.8
<i>ochoterenae</i>	-8.8	17.5	<i>magister</i>	11.4	-1.2
<i>jalapae</i>	-8.8	20.9	<i>horridus</i>	11.0	0.6
			<i>olivaceus</i>	11.9	-3.3
			<i>cautus</i>	11.3	-1.1
Group II			<i>formosus</i>	11.3	-0.9
<i>asper</i>	-14.9	-6.5	<i>malachiticus</i>	12.9	-1.4
<i>grammicus</i>	-15.3	-6.0	<i>lunaei</i>	11.7	-2.7
<i>heterolepis</i>	-15.4	-5.7	<i>lundelli</i>	12.7	-1.1
<i>megalepidurus</i>	-16.2	-5.2	<i>undulatus</i>	10.1	-2.5
<i>pictus</i>	-14.6	-6.6	<i>virgatus</i>	11.3	-1.1
<i>cryptus</i>	-15.2	-7.1	<i>occidentalis</i>	12.2	-1.5
<i>pyrocephalus</i>	-16.2	-5.1	<i>woodi</i>	12.7	-0.4
<i>nelsoni</i>	-15.5	-7.2	<i>graciosus</i>	11.7	-1.2
<i>scalaris</i>	-15.8	-5.4	<i>lineolateralis</i>	10.7	1.0
<i>aeneus</i>	-13.5	-5.2	<i>ornatus</i>	12.0	-2.4
<i>siniferus</i>	-14.1	-6.6	<i>dugesi</i>	9.4	-1.3
<i>squamosus</i>	-15.4	-7.8	<i>jarrovi</i>	13.6	-2.7
<i>carinatus</i>	-16.1	-8.5	<i>torquatus</i>	11.9	-2.7
<i>utiformis</i>	-15.0	-5.7	<i>poinsetti</i>	12.5	-1.0
<i>variabilis</i>	-14.3	-5.6	<i>cyanogenys</i>	10.9	-1.5
<i>cozumelae</i>	-14.5	-6.4	<i>serrifer</i>	10.4	-1.2
<i>teapensis</i>	-17.2	-6.2	<i>mucronatus</i>	12.7	0.3
<i>chrysostictus</i>	-13.3	-6.3	<i>bulleri</i>	14.2	-1.3

ters. With this limitation in mind, Wishart's program is extremely valuable.

As an independent check on this system, Ward's Cluster Analysis was applied to some of the data used by Smith in 1939 (pers. comm.). Because of the nature of Smith's data, only 12 characters were used: (1) snout-vent length (mm), (2) snout-occiput/snout-vent, (3) snout-ear/snout-vent, (4) length of hind leg/snout-vent, (5) length of tibia/snout-vent, (6) length of fourth toe/snout-vent, (7) length of fourth toe/length of fifth toe, (8) lamellae on fourth toe, (9) femoral pores (total both sides), (10) dorsal scales from occiput to back of thigh, (11) ventral scales from front of arm to vent, and (12) scale rows around body.

The resulting dendrogram is illustrated in Figure 8. The strong similarity between Figure 8 and Smith's phylogeny (1939) suggests that there is a similar mechanism in Ward's Cluster Analysis and the subjective thinking of classical taxonomy. This supports the conclusion that a person capable of considering 60 to 80 characters on 50 to 60 species simultaneously, would arrive subjectively at results similar to those produced by Ward's Cluster Analysis.

*Stepwise Discriminate Analysis.* The purposes of stepwise discriminate analysis are (1) to determine the validity of proposed



TABLE 14. X and Y canonical coordinates for the species in the three subgroups in Group I.

Species	X	Y	Species	X	Y
Subgroup A			Subgroup C		
<i>gadoviae</i>	-15.3	-3.3	<i>parvus</i>	1.4	3.1
			<i>maculosus</i>	1.2	3.3
Subgroup B			<i>ochoterenae</i>	0.5	5.1
<i>merriami</i>	12.1	-5.7	<i>jalapae</i>	-0.2	2.0
<i>couchi</i>	12.3	-4.2			

groups, (2) to determine the relative diagnostic value of each character, and (3) to classify individuals according to the proposed groups. The stepwise discriminate analysis computer program published by Dixon (1967) considers one character at a time according to F-ratios (variation between groups/variation within groups). Each step "includes" the remaining character with the highest F-ratio. At each step the species are classified according to all the included characters. As more characters are included, the differences between group means become more significant (as indicated by a U-statistic and an approximate F-value), and more individuals are properly classified.

Dixon's program produces (1) means for each group and overall means for each character, (2) standard deviations for each character in each group, (3) within-group covariance matrix, (4) within-group correlation matrix, (5) detailed results for each "step."

At each step a new variable is included and the program prints the F-ratios (and degrees of freedom) for all variables included and not included. The program also prints a U-statistic with degrees of freedom for an estimate of the significance of group separation. Since the U-statistic becomes extremely small and exceeds the capacity of most charts, the program computes an approximate F that, with its degrees of freedom, can show the confidence level for overall group separations.

Dixon's program also produces an F-matrix in which F-ratios are computed for every possible combination of two groups. If the characters included provide good overall separation but fail to distinguish between two groups, this matrix will quickly show which pairs are not separated at .9, .99, and .999 levels of significance. (F tables are not included in the printout.)

This program also produces canonical functions for each step. These functions are then used to classify all species according to the information in the included characters. As more characters are included, the percent of species properly classified increases if the original groupings are valid. At the end of the printout the "distance" is computed from each species to the center (centroid) of each group. Posterior probability for inclusion in each group is also computed for each species. The computer was instructed to "include" characters only if their F-ratio exceeded 1.0 and to "remove" characters if their F-ratio fell below 0.5. A summary of variables "in-

TABLE 15. X and Y canonical coordinates for the species in the five subgroups in Group II.

Species	X	Y	Species	X	Y
Subgroup A			Subgroup D		
<i>asper</i>	-30.0	7.5	<i>siniferus</i>	101.7	-1.2
<i>grammicus</i>	-32.2	5.6	<i>squamosus</i>	102.2	-0.1
<i>heterolepis</i>	-31.0	7.6	<i>carinatus</i>	101.7	0.1
<i>megalepidurus</i>	-32.1	9.0	<i>utiformis</i>	101.1	0.5
<i>pictus</i>	-30.0	6.1	Subgroup E		
<i>cryptus</i>	-33.0	6.7	<i>variabilis</i>	-57.3	-6.5
Subgroup B			<i>cozumelae</i>	-57.3	-6.0
<i>pyrocephalus</i>	-9.3	-6.5	<i>teapensis</i>	-59.1	-4.8
<i>nelsoni</i>	-9.7	-7.4	<i>chrysostictus</i>	-56.8	-5.9
Subgroup C					
<i>scalarus</i>	14.6	-3.3			
<i>aeneus</i>	16.1	-1.2			

cluded" or "removed" including F-ratios and U-statistics is printed near the end of the printout. Then the program tabulates (1) eigenvalues, (2) cumulative proportion of total dispersion, (3) canonical correlations, (4) coefficients for canonical variables, (5) canonical variables evaluated at group means, and (6) graph coordinates for the first and second canonical variables for each species in each group. The program terminates with a graphic representation of all species on the first two canonical variables.

*Canonical Analysis.* The canonical analysis (a part of Dixon's program) computes a pair of linear coefficients for each character so that the greatest separation of groups can be displayed on a two-dimensional graph. For example, Figure 9 shows groups A and B plotted on characters p and q. To reduce the illustration from two dimensions to one, all points must be projected onto a single line. Line X would show more information about groups A and B than would line Y. In accordance with this idea, the canonical analysis rotates an imaginary plane through a multidimensional hyperspace until the best separation of groups is displayed. The lists of canonical functions are used to classify additional individuals according to the originally proposed classification and the "best" characters.

## RESULTS

*Skulls.* Skulls of 13 species of the genus *Sceloporus* are illustrated in Figure 10.

*Cluster Analysis.* Ward's cluster analysis was applied to the following sets of variables:

1. External characters 1-40 (Fig. 11).
2. Skull characters 41-80 (Fig. 12).
3. External and skull characters 1-80 (Fig. 13).
4. External, skull, and distribution characters 1-82 (Fig. 14).
5. External, skull, distribution, and display characters (Fig. 15).
6. External, skull, distribution, and karyological characters (Fig. 16).

TABLE 16. X and Y canonical coordinates for the species in the five subgroups of Group III.

Species	X	Y	Species	X	Y
Subgroup A			Subgroup C		
<i>spinosus</i>	103.9	-3.9	<i>undulatus</i>	-90.4	25.2
<i>edwardtaylori</i>	104.6	-5.3	<i>virgatus</i>	-90.7	26.3
<i>melcinorhinus</i>	103.1	-5.8	<i>occidentalis</i>	-91.7	27.0
<i>clarki</i>	102.5	-4.2	<i>woodi</i>	-92.1	26.9
<i>orcutti</i>	102.4	-5.6	<i>graciosus</i>	-91.3	28.1
<i>magister</i>	104.9	-5.8	Subgroup D		
<i>horridus</i>	104.3	-4.4	<i>jarrovi</i>	-22.5	0.32
<i>olivaceus</i>	102.2	-4.6	<i>ornatus</i>	-23.8	2.6
<i>cautus</i>	104.7	-3.7	<i>dugesi</i>	-23.9	0.2
Subgroup B			<i>lineolateralis</i>	-22.5	3.1
<i>formosus</i>	-158.3	-21.0	Subgroup E		
<i>malachiticus</i>	-158.4	-19.7	<i>torquatus</i>	67.5	1.6
<i>lunaei</i>	-158.4	-22.5	<i>poinsetti</i>	68.7	1.7
<i>lundelli</i>	-157.1	-19.5	<i>cyanogenys</i>	67.0	0.8
			<i>serrifer</i>	69.9	0.6
			<i>mucronatus</i>	66.1	1.0
			<i>bulleri</i>	68.0	1.1

7. External, skull, distribution, display, and karyological characters (Fig. 17).  
8. Distribution, display, and karyological characters (Fig. 18).

ANALYSIS AND CONCLUSIONS

*Species Groups.* The minor differences among these eight dendrograms were resolved subjectively to produce three major divisions and 13 species groups (Table 2). Careful examination will reveal the similar patterns generated by different sets of data. Figure 18 shows that distribution, display, and chromosome characters produce results similar to those produced by external and osteological characters. This increases our confidence in Table 2 and demonstrates the taxonomic value of zoogeography, behavior, and karyology.

*Stepwise Discriminate Analysis.* Dixon's stepwise discriminate analysis program cannot consider as many as 82 characters in one run. It was therefore used with external characters alone (1-40) and skull characters alone (41-80). For both studies the program was run four times to consider the three groups and their subgroups. The number of characters in the data set was reduced by eliminating those characters with consistently small F-ratios. The characters removed were numbers 2, 5, 15, 18, 19, 25, 42, 45, 46, 51, 65, 68, 73, 76, and 78. With the inclusion of latitude and longitude, this program then evaluated 66 characters.

Table 3 shows the results of stepwise discriminate analysis of the three groups in the genus *Sceloporus*. This table shows that when characters are considered according to F-ratios, eight characters are sufficient for correct classification of all species: (1) size of caudal scales, (2) degree of compression of tail, (3) width of

dorsal scales, (4) length of frontal scale, (5) ventrals between medial limits of femoral pores, (6) length of fourth toe, (7) head shields in contact with interparietal, and (8) length of prefrontal bone. The first eight characters contribute variation significant at the .99 level. Of the 39 most diagnostic characters (F-ratio greater than 1.0), 10 are osteological, 1 is geographical (longitude), and 28 are external. The null hypothesis that the three groups are not different is rejected at the .999 level after consideration of the first character (number of caudal scales equal to one head length). The same hypothesis is rejected at the .999 level with respect to any combination of two groups. The eight diagnostic characters with means and standard deviations are shown in Table 4.

Table 5 shows the results of stepwise discriminate analysis for the three subgroups of group I. Two characters are sufficient to classify the species into their subgroups. Both characters contribute variation significant at the .999 level. The first is a measure of the degree of compression of the tail, and the second is the number of ventrals. At every step, the separation of means is significant at the .999 level after inclusion of the second character. Of the six most diagnostic characters (F-ratio greater than 1.0), two are osteological and four are external. Table 6 shows the means and standard deviations of the first two characters.

Tables 7, 8, and 9 show the results of stepwise discriminate analysis of the five subgroups of group II. Four characters are sufficient for 100-percent correct classification of all species: (1) the relative width of the supraoculars, (2) the number of lamellae on the fourth toe, (3) the degree of compression in the tail, and (4) a measure of the relative width of the basisphenoid bone. Of the 13 most diagnostic characters (F-ratio greater than 1.0) 4 are osteological, 1 is geographical (latitude), and 8 are external. The approximate F (U-statistic) for overall separation of means is significant at the .999 level for every step.

Tables 10, 11, and 12 show the results of stepwise discriminate analysis of the five subgroups within group III. Six characters are sufficient for correct classification: (1) the size of ventral scales in the vent region, (2) latitude, (3) the number of dorsals equal to the length of the head, (4) the compression of the tail, (5) the size of dorsals near the interparietal scale, and (6) the shape of the ectopterygoid bone. The separation of the subgroups of group III is as significant as is the separation in group II. Of the 24 most diagnostic characters (F-ratio greater than 1.0) 8 are osteological, 1 is geographical (latitude), and 15 are external.

Tables 3 to 12 show that the groups and subgroups proposed in Table 2 are distinct at the .999 level of confidence according to the characters used in this study. These tables also show which characters are most diagnostic among the groups.

*Canonical Analysis.* Figure 19 shows the first two canonical dimensions for the species in each major group. Table 13 gives the  $x$  and  $y$  coordinates for each species. This canonical separation gives

strong support to the conclusion that each of the three groups is monophyletic and should be given taxonomic recognition.

Figures 20, 21, and 22 and Tables 14, 15, and 16 indicate that the subgroups of each major group are also distinct phenetic units with no overlap.

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